

# LOWER CRETACEOUS DIPLOBELINID BELEMNITES FROM THE ANGLO-PARIS BASIN

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**ABSTRACT.** Re-evaluation of belemnites belonging to the suborder Diplobelina Jeletzky, 1965 has resulted in erection of the new genera *Vectibelus* (based on *Conoteuthis vectensis* Spath, 1939) and *Chalalabelus* (based on *Conoteuthis remiei* Spath, 1939). A specifically indeterminate representative of *Chalalabelus* is described from the Barremian of Speeton, England. The genera *Vectibelus* gen. nov. and *Conoteuthis* d'Orbigny, 1842 are characterized by thin, skin-like guards, which are different from the stout, adapically rounded guards of *Chalalabelus* gen. nov. and *Diplobelus* Zittel, 1868. *C. dupiniana* d'Orbigny, 1842 is redescribed on the basis of new material from the French and English Aptian. '*Conoteuthis cantiana* Spath, 1939 from the Albian of Folkestone, England is redescribed and assigned to the Central Russian genus *Pavloviteuthis* Shimansky, 1957. This genus is redescribed and interpreted as a morphologically conservative descendant of the unknown, early Late or Mid-Jurassic rootstock of the Diplobelina. This hypothetical rootstock is assumed to be derived from *Coeloteuthis?* ex gr. *palliatius* (Dumortier, 1869). *Diplobelus* is interpreted as an early offshoot of this rootstock and the direct ancestor of *Chalalabelus*. *Conoteuthis* and *Vectibelus* are interpreted as direct descendants of *Pavloviteuthis*, which are not directly related to other diplobeline genera.

THE suborder Diplobelina was erected by Jeletzky (1965, 1966) to hold morphologically peculiar and apparently phylogenetically isolated true belemnites grouped around the genus *Diplobelus* Naef, 1926. The revision of all known genera of Diplobelina revealed a rather unsatisfactory state of knowledge of the suborder (Jeletzky, 1966, p. 149). A subsequent search in collections of most of the larger museums of west Europe and England and in some private palaeontological collections of these countries produced some diplobeline belemnites. Although meagre numerically, this material was found to be unexpectedly diverse and to include new, morphologically peculiar taxa. This paper summarizes the principal results of this study.

## SYSTEMATIC PALAEOLOGY

### Suborder DIPLOBELINA Jeletzky, 1965

*Diagnosis.* Belemnitida with an adorally tapering proostracum which has the shape of short dagger blade with an acute or very narrowly rounded tip; the flanking hyperbolar zones of belemnitid type converge gradually toward the mid-dorsum until they merge at the tip of proostracum; suture lines more sinuous than in any other Belemnitida known with a pronounced, angular to broadly rounded dorsal saddle and a feeble to barely suggested but usually narrow ventral lobe; septa usually considerably to much more crowded than those of other Belemnitida suborders with the height of septal camerae varying between one-sixth (very rarely) and one-twentieth of their length (measured dorso-ventrally); axis of the apical half of mostly breviconic phragmocone tends to be markedly incurved endogastrically; guard is either short, stout, and bluntly rounded adapically or rudimentary. Ranges from the late Jurassic (Tithonian) to latest Cretaceous (Maastrichtian).

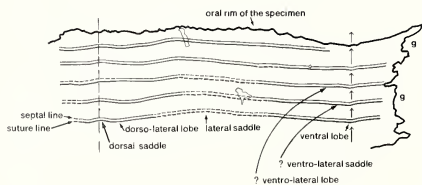
*Geographic range.* The oldest representatives (*Diplobelus*) are known only in the Tithonian of the Alpine and Crimean-Caucasian regions. In the mid- to late Early Cretaceous (Hauterivian-Albian) and earliest Late Cretaceous (Cenomanian) Diplobelina are only known from the African and the Near Eastern regions of the

Tethyan Realm (Lebanon, Mozambique) and the southern outskirts of the Boreal Realm in Europe (e.g. Anglo-Paris Basin, eastern Russia). In the latest Cretaceous (early Maastrichtian) the *Diplobelina* are only known on the Pacific Coast of North America (a new genus in Canada to be described elsewhere).

**Discussion.** The diagnosis of *Diplobelina* given above is an emendation of that given previously (Jeletzky, 1966, p. 149). Neither the presence of longitudinal mediadorsal keel nor the pronounced adventral sloping of the suture lines can be considered diagnostic of the suborder following the revision of the genus *Pavloviteuthis* in this paper. The same is true of the presence of the chevron-like dorsal saddle which occurs only in those genera which possess the mediadorsal keel. Finally, the traditionally stressed (since Zittel, 1868), apparent lack of the radially prismatic structure of the guard appears to be a result of post-mortem weathering in those forms where it is reduced to a very thin. *Belemnoteuthis*-like envelope. Gustomessov (1976, pp. 65, 66) points out that drawings of the holotype of *Conoteuthis dupiniana* (d'Orbigny, 1842, pl. 12, figs. 1-4) feature a well-developed, completely closed Aulacocerida-like living chamber. All *Conoteuthis* specimens studied are fully septate phragmocones and so do not offer any evidence either for or against the existence of such a living chamber. However, as noted by Naef (1922, p. 279), d'Orbigny (1842, p. 379, expl. of pl. 12, fig. 2) states that the nonchambered part of the holotype is restored. This statement and the manner in which the living chamber and the rhachis-like proostracum of *C. dupiniana* are outlined in d'Orbigny's (1842, pl. 12, figs. 1, 2, 4) drawings leave no doubt that their existence was only assumed in accordance with erroneous ideas then prevalent (see Jeletzky, 1966, pp. 109, 110 for further details). This conclusion is confirmed by the circumstance that d'Orbigny's (1842, pl. 12, fig. 9) reconstruction of a complete belemnite shell includes a living chamber similar to that sketched in his reconstruction of *C. dupiniana*. It is concluded therefore, contrary to Gustomessov (1976, pp. 65, 66), that *C. dupiniana* and all other representatives of *Diplobelina* lacked the living chamber.

Many workers (Jeletzky, 1966, p. 149) have placed all diplobeline belemnites in the family Belemnoteuthidae Zittel, 1895. Jeletzky (1966, pp. 144, 149) admitted the affinity of Belemnoteuthidae and *Diplobelina* but insisted on their independence because of the presence of several important morphological distinctions. Jeletzky's comparison of *Diplobelina* and Belemnoteuthidae was incomplete because of a poor preservation of all *Belemnoteuthis* guards then available. This defect will be remedied here using some previously unavailable, exceptionally well-preserved guards of *B. antiqua* Pearce, 1847 from the Kellaway Rock, Wiltshire (e.g. Pl. 24, fig. 2A-G, text-fig. 1).

The mediadorsal sculpture of *Belemnoteuthis* guard is more similar to that of the *Conoteuthis* and other diplobeline belemnites provided with a mediadorsal thickening of the guard than usually believed. This *Belemnoteuthis* sculpture is habitually described as consisting of two longitudinal mediadorsal keels separated from each other by a mediadorsal furrow (Naef, 1922, p. 277; Jeletzky, 1966, p. 78, pl. 16, fig. 2). The mediadorsal sculpture of *Conoteuthis* and other *Diplobelina* is, in contrast, described as a strong longitudinal, mediadorsal keel or ridge (d'Orbigny, 1842, p. 376; Naef,

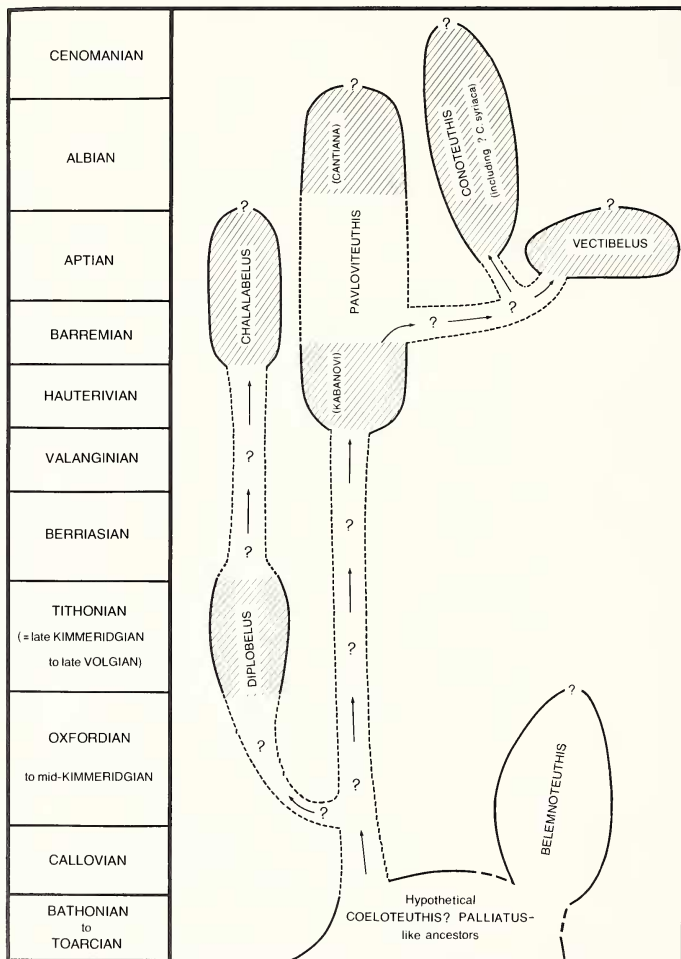


TEXT-FIG. 1. Camera-lucida drawing of the five most oral suture lines and associated septal lines of the specimen of *Belemnoteuthis antiqua* Pearce 1847 reproduced in Pl. 24, fig. 2A-G,  $\times 6$ . Preservation is poor in part and the reproduction is diagrammatic whenever the lines are shown in dashed lines. Upward-directed arrows mark the position of the mid-venter (ventral lobe) while the vertical dashed line marks the position of the mid-dorsum (dorsal saddle). Arrows are used to indicate dorso-lateral lobe and lateral saddle, and to suggest the location of ventro-lateral lobe and saddle. Irregular patches of the thin guard (g) are also indicated.

1922, p. 279; Spath, 1939, p. 3; Jeletzky, 1966, p. 149). However, this keel is also subdivided in two by a mediadorsal longitudinal furrow in all diplobeline genera where it occurs (e.g. in *Conoteuthis* and *Vectibelus*; Pl. 21, fig. 1K; Pl. 24, fig. 1G, I; text-figs. 3, 4, 11). The median longitudinal furrow, which separates the dorsal keels, of *Belemnoteuthis antiqua* (Pl. 24, fig. 2C) is considerably deeper and wider than the equivalent furrow of *Diplobelina* (e.g. Pl. 24, fig. 1I). The flanking ridges are likewise considerably wider and more heavily built than the equivalent ridges of the diplobeline keel. Conversely, the bulge of the guard bearing the so-called keels and the median furrow of *Belemnoteuthis* is considerably less prominent than the bulge comprising the diplobeline keel (compare Pl. 24, fig. 1F, G and text-fig. 11 with Pl. 24, fig. 2C, F). All elements of these two structures are, nevertheless, sufficiently similar to treat the mediadorsal structure of *Belemnoteuthis* guard as a mediadorsal keel with a superposed furrow and ridges instead of its conventional interpretation as two keels separated by a mediadorsal furrow. Only the outer, sloping longitudinal zones of a diplobeline keel (*C. dupiniana*, Pl. 21, fig. 1K, and *Vectibelus vectensis*, Pl. 24, fig. 1G, I; text-fig. 11) are absent in the mediadorsal apical keel of *B. antiqua* (Pl. 24, fig. 2F, G) as its heavily built, round-topped flanking ridges merge immediately into steep slopes (instead of moderate slopes of a diplobeline keel) of the keel (Pl. 24, fig. 2F, G).

The narrow, only slightly elevated but regularly rounded, dorsal saddle of the *Belemnoteuthis* suture line, as shown by text-fig. 1, is relatively much more narrow than the still less elevated dorsal saddle of *Pavloviteuthis* (text-fig. 8). However, it is similarly wide to more elevated, different-shaped dorsal saddles of other diplobeline genera. The dorsal saddle of *Belemnoteuthis* grades imperceptibly into a wide, slightly depressed and flat-bottomed dorso-lateral lobe, which occupies most of the dorsal quadrant and some of the dorso-lateral quadrant of the phragmocone. This lobe is followed, in turn, by a very wide, but only slightly arched, lateral saddle, which occupies the remainder of the dorso-lateral quadrant and the adorsal three-fifths of the flank. The adorsal slope of this saddle is shorter and steeper than any other part of it. This slope is followed by a relatively very long, approximately flat top of the saddle, which may be slightly depressed in the middle. This depression may represent a barely discernible, wide lateral lobule within the lateral saddle. However, this suggestion must be confirmed by a study of additional, better-preserved specimens. The relatively gentle and long adventral slope of the lateral saddle occupies the middle part of the flank. It merges into a slightly depressed, wide ventro-lateral part of the suture line, which is interpreted tentatively as the ventro-lateral lobe (text-fig. 1). A slight but relatively narrow elevation separating this questionable ventro-lateral lobe from the ventral lobe is interpreted, equally tentatively, as the ventro-lateral saddle. Whenever the adventral slope of this ?ventro-lateral saddle is clearly defined it merges into a shallow but relatively very narrow and broadly U-shaped ventral lobe. This ventral lobe is more narrow and better delimited than that of *Diplobelina* (compare text-figs. 5, 8, 10). The suture line of *Belemnoteuthis* is only slightly adventrally inclined forming an angle of about 85 degrees with the longitudinal axis of its essentially straight shell (Pl. 24, fig. 2B, C, F).

*Phylogenetic remarks.* Available diplobeline material is scarce and widely scattered geographically and stratigraphically, which precludes any definite conclusions about the origin of the suborder and the relationships of its individual genera. The following phylogenetic observations are accordingly tentative. The genus *Pavloviteuthis* Shimansky, 1957 is judged to be the most primitive diplobeline genus known. Its phragmocone and guard are devoid of a mediadorsal ridge and the dorsal saddle of its suture line is broadly rounded and flat-topped. The phragmocone of *Pavloviteuthis* is moderately slender, only slightly adventrally incurved, and has an egg-shaped rather than an adorsally sharpened cross-section. Finally, the tip of its adorally tapering, concave-flanked proostracum appears to be very narrowly rounded instead of sharpened. Therefore, it appears to be morphologically transitional to the spatulate proostracum of the Belemnitina. Except for this morphologically, and presumably phylogenetically, primitive but already diplobeline shape of the proostracum, the shell morphology of *Pavloviteuthis* is essentially Belemnitina-like. The resemblance of the mediadorsal sculpture of *Belemnoteuthis* to that of *Diplobelina* supports my previous opinion (Jeletzky, 1966, pp. 142, 149, 150, fig. 15) on their general affinity. However, it appears impossible to



TEXT-FIG. 2. Suggested phylogenetic relationships and time ranges of the presently known Diplobelina genera. Time intervals from which at least some representatives of the genera concerned are known, are obliquely ruled and indicated in solid lines. Intervals from which their representatives are unknown but during which they presumably existed, are left blank and are outlined in dashed lines.



derive the Diplobelina directly from the Belemnoteuthididae, or to include that family in the suborder, for the following reasons:

1. Unlike the Diplobelina, Belemnoteuthididae have an entirely Belemnitina-like proostracum (Jeletzky, 1966, pp. 144, 149, pl. 16, fig. 2) and a cuplike protoconch (Makowski, 1952, pp. 46, 47, fig. 11A).

2. The suture line of *Belemnoteuthis* is more complex than that of the most primitive diplobeline genus, *Pavloviteuthis*, which has only two saddles and two lobes. The *Belemnoteuthis* suture line compares with those of morphologically more advanced diplobeline genera, such as *Conoteuthis* s. restr., *Vectibelus*, *Chalalabelus*, and possibly *Diplobelus*, which otherwise differ in the more elevated, mostly chevron-like character of the dorsal saddle and other taxonomically important features.

3. The median furrow and flanking ridges of mediodorsal keel common to Belemnoteuthididae and Diplobelina are only known in morphologically, and presumably phylogenetically, advanced diplobeline genera, but not in *Pavloviteuthis*.

All Belemnitina-like morphological features of *Pavloviteuthis* ally it with the early, morphologically most primitive representatives of the Belemnitina centred in *Coeloteuthis? palliata* (Dumortier, 1869). This coeloteuthid form-group, which presumably is a new genus, is the only one in the Belemnitina known to possess a rudimentary, envelope-like guard, the surface of which is devoid of the triple lateral longitudinal furrows. The cross-section of the guard of *C.? palliata* is pear-shaped, with a distinctly narrowed dorsal segment (Dumortier, 1869, pl. V, fig. 14). *C.? palliata* are, therefore, believed to be the ultimate ancestors of the Diplobelina via some morphologically transitional (i.e. more *Pavloviteuthis*-like) forms yet to be found in the intervening Toarcian to Valanginian rocks. The Hauterivian *Pavloviteuthis kabanovi* appears to be a relatively little-changed descendant of that hypothetical ancestral stock of the Diplobelina. The morphologically more advanced but older (i.e. Tithonian) *Diplobelus* is interpreted as a specialized early offshoot of the hypothetical lineage connecting *Coeloteuthis? ex gr. palliata* with *Pavloviteuthis* (text-fig. 2).

Because of their pronounced morphological distinctions from *Pavloviteuthis*, the Belemnoteuthididae appear to be an independent offshoot of the same *Coeloteuthis? ex gr. palliata* stock that produced Diplobelina. The Belemnoteuthididae originated from that stock in pre-Callovian time and before the origination of the Diplobelina (text-fig. 2). This is indicated by the fact that, unlike the most primitive Diplobelina, they have retained such a fundamental character of the Belemnitina as the spatulate proostracum. They must therefore be retained in this suborder, contrary to the opinion of Donovan (1977, p. 31). Jeletzky (1966, p. 145) observed that the cuplike shape of the *Belemnoteuthis* protoconch is a relatively low-ranking feature, which does not justify its exclusion from the Belemnitina. The lack of information about the shape of the protoconch of *Coeloteuthis*, including *C.? palliata* makes it impossible to say whether the cuplike protoconch of *Belemnoteuthis* was inherited unchanged from its *C.? palliata*-like ancestors or represents a secondary, presumably adaptive, modification of an originally subsphaeroidal protoconch. Therefore, it cannot be decided whether or not the sphaeroidal protoconch of *Diplobelus* (Jeletzky, 1966, p. 150) is a homoeomorphic development within the Diplobelina paralleling that characteristic of the more advanced Belemnitina, or a primitive feature inherited from the common ancestor of the Diplobelina and the Belemnoteuthididae.

Of the other typical, presumably specialized diplobeline genera, *Chalalabelus* gen. nov. may well be a direct descendant of *Diplobelus*, as already suggested by Spath (1939, p. 2). These two genera share a massive, adapically rounded, completely unornamented guard, mediodorsal keel of the phragmocone, and the chevron-shaped dorsal saddle of the suture line. Furthermore, the time ranges of these two genera are compatible with their suggested ancestor-descendant relationship (text-fig. 2). The short and wide, strongly adventrally incurved phragmocone of *Chalalabelus* appears to be an independent development which mimics the phragmocone of *Conoteuthis* and *Vectibelus*. *Conoteuthis* and *Vectibelus* gen. nov., which have a reduced, skin-like guard, which resembles that of *Pavloviteuthis*, and a short and wide, strongly adventrally incurved phragmocone resembling that of

*Chalalabelus* gen. nov., are interpreted tentatively as another, considerably later offshoot of the *Pavloviteuthis* lineage. Unlike *Diplobelus* and *Chalalabelus* gen. nov., the mediadorsal keel of these two genera is expressed on both the phragmocone and the surface of the guard. The *Conoteuthis-Vectibelus* gen. nov. stock coexisted with the *Pavloviteuthis* lineage, as the latter is already known to range from the Hauterivian to the Aptian inclusive and may have lasted into the younger beds (text-fig. 2). The Cenomanian *Conoteuthis? syriaca* (Roger, 1944) is tentatively assigned herein to the *Conoteuthis-Vectibelus* gen. nov. stock.

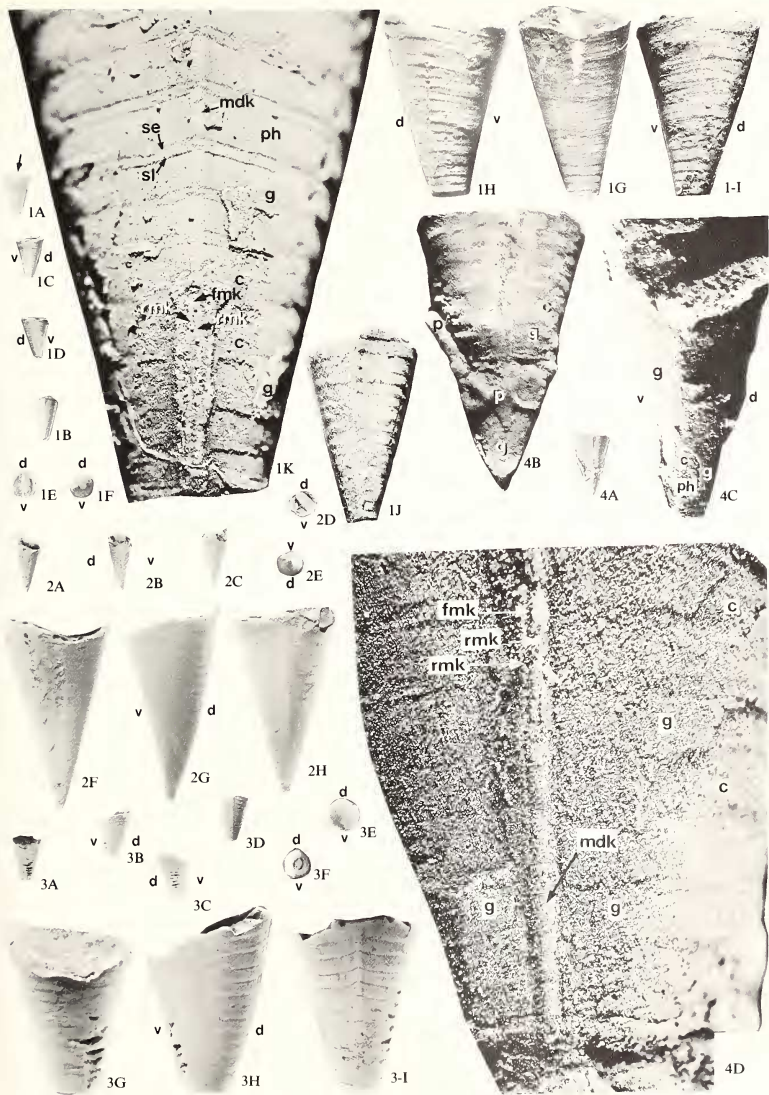
The poorly known and stratigraphically uncertain genus *Amblybelus* Naef, 1922 was assigned to the family Diploconidae (later Diplobelinae) by its author (see Naef, 1922, pp. 279, 280). This genus, based on *Belemmites obtusus* de Blainville, 1827, is transferred herewith to the family Belemnoteuthidae. This reassignment is based on the allegedly very broad and flat, generally cup-like protoconch of the *Amblybelus*. This genus differs markedly from the *Belemnoteuthis* in its fairly thick guard, comparable to that of *Brachybelus*.

#### Family DIPLOBELIDAE Naef, 1926

The family name Diploconidae Naef, 1922 was based on the preoccupied generic name *Diploconus* Zittel, 1868. It was replaced by Diplobelidae in a subsequent paper where that genus was renamed (Naef, 1926, p. 4). The validity of all lineages of Diplobelina suggested in the preceding section being rather doubtful, no families, or even subfamilies, are being erected for them in this paper. The family Diplobelidae remains, therefore, the only known family of Diplobelina, although its scope is being expanded considerably as compared with Naef's (1922, p. 278) original concept. Its diagnosis is the same as that of the suborder.

#### EXPLANATION OF PLATE 21

- Fig. 1A-K. *Conoteuthis dupiniana* d'Orbigny, 1842. Loc. No. 927/1. Muséum de Histoire Naturelle, Genève, Switzerland. Aptian, Gurgy (Yonne), France. A, ventral view,  $\times 1$ . White line (arrow) marks the medio-ventral plane. B, dorsal view,  $\times 1$ . The mediadorsal keel extends all the way to broken apical end of the specimen. C, left lateral view (in relation to the venter),  $\times 1$ . D, right lateral view (in relation to the venter),  $\times 1$ . E, cross-section of the alveolar end,  $\times 1$ . F, cross-section of the apical end,  $\times 1$ . The same legend as in fig. 1E. G-J, the same views and legends as in fig. 1A-D but  $\times 4$  to elucidate fine structural details not visible in the latter photographs. K, dorsal view of the apical half of the specimen,  $\times 17$ . Patches of conotheca (c) and thin guard (g) are locally superimposed on the exposed internal cast of the phragmocone (ph); se—septal line; sl—suture line; mdk—preserved fragment of mediadorsal keel; fmk—central furrow of mediadorsal keel; rmk—flanking ridges of mediadorsal keel; v—venter; d—dorsum.
- Fig. 2A-H. *Conoteuthis dupiniana* d'Orbigny, 1842. B.M. (N.H.) C.46812. Aptian, Gurgy, near Auxerre (Yonne). A, ventral view,  $\times 1$ . B, left lateral view (in relation to the venter),  $\times 1$ . C, dorsal view,  $\times 1$ . D, oral view of the alveolar end,  $\times 1$ . E, apical view of the apical end,  $\times 1$ . F, the same view as in fig. 2A but  $\times 4$  to show fine structural details. G, right lateral view,  $\times 4$ . H, dorsal view,  $\times 4$ . The mediadorsal keel extends almost to the apical end of this nearly complete specimen and its apparent absence at its apex may be due to poor preservation (compare text-fig. 3).
- Figs. 3A-I. *Conoteuthis dupiniana* d'Orbigny, 1842. B.M. (N.H.) C.37881. Aptian, Gurgy, near Auxerre (Yonne). A, ventral view,  $\times 1$ . B, right lateral view (in relation to the venter),  $\times 1$ . C, left lateral view (in relation to the venter),  $\times 1$ . D, dorsal view,  $\times 1$ . E, cross-section of the oral end,  $\times 1$ . F, cross-section of the apical end,  $\times 1$ . G, ventral view,  $\times 4$  to show fine structural detail not visible in fig. 3A. H, right lateral view (in relation to the venter),  $\times 4$ . I, dorsal view,  $\times 4$ .
- Fig. 4A-D. *Conoteuthis dupiniana* d'Orbigny, 1842. Loc. No. 927/2. Data as for fig. 1. Strongly deformed guard covered by conotheca (c) with patches of thin guard (g) which thickens adapically. Bleds of pyrite (p) cover the specimen's surface locally. A, dorsal view,  $\times 1$ . Mediadorsal keel absent on one-quarter of specimen covered by the guard. Few, most apical chambers of the phragmocone broken off (compare fig. 4C). B, same,  $\times 4$ , to show fine structural detail. C, right lateral view of the apical third,  $\times 12$ . Thickness of guard (g) increases on the most apical part of the specimen (compare fig. 4B), as shown adventrally of the midflank which exposes the surface of chambered phragmocone (ph) with specks of conotheca (c). D, dorsal view of the mediadorsal segment of the oral half of the specimen visible in fig. 4A, B,  $\times 18$  to show fine structural details. Explanations of letters as in fig. 1K.



JELETSKY, Cretaceous belemnites

## Genus CONOTEUTHIS d'Orbigny, 1842

*Diagnosis.* Diplobelidae combining feebly to markedly but always regularly endogastrically incurved phragmocone with paper-thin, sheath-like guard, which only thickens slightly in the proximity of the protoconch; longitudinal mediiodorsal keel of the phragmocone begins in a close proximity of shell's apex and extends to its oral end gradually increasing in prominence orolward; this keel is superimposed on the tops of dorsal saddles of the suture lines which are broadly rounded initially but become sharp-topped and angular further adorally; the keel is also expressed on the guard's surface where it is ornamented by a median furrow and flanking ridges. Range: Mid- to late Early Cretaceous (Aptian-Albian) and possibly earliest Late Cretaceous (Cenomanian).

*Geographical range.* *Conoteuthis* s. restr. has been found only in the Anglo-Paris Basin. However, the insufficiently understood *Conoteuthis? syriaca* (Roger, 1944) from the Cenomanian of Lebanon may well be a true *Conoteuthis* as restricted herein.

*Discussion.* The above diagnosis of *Conoteuthis* is an emendation of that given previously (Jeletzky, 1966, p. 151), necessitated by the removal of *C. vectensis* Spath, 1939 and *C. renniei* Spath, 1939 from the genus. The 'extremely short, rapidly expanding phragmocone having apical angle (30 degrees in type species) greater than in other members of family' (Jeletzky, 1966, p. 151) and the markedly adventrally inclined orientation of suture lines have now lost their diagnostic value. They are just as characteristic of the genera *Vectibelus* gen. nov. and *Chalalabelus* gen. nov. as they are of the *Conoteuthis* in the restricted sense. The phragmocone that is 'commonly more or less irregularly curved ventrally' and the mediiodorsal keel that is restricted to the anterior part of the phragmocone are now diagnostic features of *Vectibelus* gen. nov.; they are unknown in *Conoteuthis* s. restr. The thin to very thin, investment-like guard is no longer a characteristic feature of the *Conoteuthis*, as it occurs in *Pavloviteuthis cantiana* (Spath, 1939) and *Vectibelus vectensis* (Spath, 1939) as well. As recognized by L. Bairdow (pers. comm. 1964) and Jeletzky (1966, p. 151), Spath (1939, p. 2) erred in assuming that the *C. dupiniana* possessed a *Diplobelus*-like guard essentially similar to the massive and adapically rounded guard of his '*C. renniei*' from Mozambique. However, Spath (loc. cit.) was right when stating that the former species: 'has been established on an isolated phragmocone'. The presence of a strongly reduced, investment-like guard in *Conoteuthis* is documented for the first time below in the description of *C. dupiniana*.

The suture line of *Conoteuthis* differs markedly from the suture lines of the *Pavloviteuthis* and *Diplobelus* in the presence of a strongly elevated, chevron-like dorsal saddle in advanced growth stages. However, it is similar to the suture lines of the *Vectibelus* and *Chalalabelus* in this respect. This suture line differs from those of the *Pavloviteuthis* and *Diplobelus*, but not from those of the *Vectibelus* and *Chalalabelus*, in being markedly inclined adventrally. Finally, the *Conoteuthis* suture line consists of three lobes and three saddles (text-fig. 5) while the sutures of *Pavloviteuthis* and *Vectibelus* appear to consist of two saddles and two lobes only (text-figs. 8, 10). This distinction needs confirmation through a study of additional representatives of the latter two genera. The shallow but narrow, round-bottomed, ventral lobe in the *Conoteuthis* suture line may not be taxonomically significant on the generic level. This lobe is not evident in at least one of the studied examples of *C. dupiniana* (e.g. Pl. 25, fig. 4r) whilst the straight, ventral part of the single example of *V. vectensis* (Pl. 24, fig. 1r, text-fig. 10) appears to form a distinct, albeit slight, ventral lobe at least in a couple of its best visible orolmost suture lines. *Pavloviteuthis* sutures show a pronounced ventral lobe, which is much wider than that of *Conoteuthis* (compare text-figs. 5, 8). So far as known, only *Vectibelus* exhibits the same small distance (about one-sixth of the height of the camerae concerned) between the suture line and the septal line, which is characteristic of *Conoteuthis* (compare text-figs. 5, 10). This distance is considerably greater in *Pavloviteuthis* (text-figs. 8, 9) and the same appears to be true of *Diplobelus* (Pl. 25, fig. 1A, B). No data is available for *Chalalabelus*. The transverse corrugations of the phragmocone and conotheca observed in *Conoteuthis* are equally well developed in the exposed most apical part of the phragmocone of *P. cantiana* (Pl. 23, fig. 1B, E). Therefore, they are believed to be characteristic of all diplobeline genera.

The sculpture of the mediodorsal keel ornamenting the guard of *Conoteuthis* (*C. dupiniana* below) differs from that of the *Vectibehus* keel in the following details: (1) The median longitudinal furrow of the *Conoteuthis* keel is relatively more narrow and round-bottomed; (2) The flanking longitudinal ridges of *Conoteuthis* are about as wide as the median furrow, round-topped and merge imperceptibly into the latter; and (3) The slopes of the *Conoteuthis* keel are relatively considerably more narrow at the corresponding growth stages. The mediodorsal keel of the *Conoteuthis* begins in close proximity to the apex of the shell while that of the *Vectibehus* begins in the middle part of the shell.

*Conoteuthis dupiniana* d'Orbigny, 1842

Plate 21, figs. 1-4; Plate 25, fig. 4

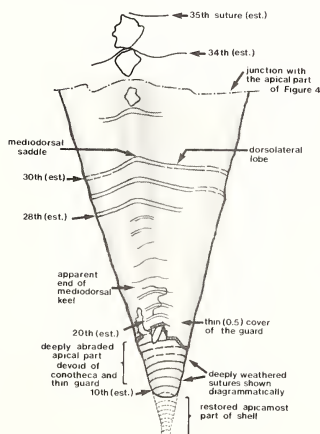
1842 *Conoteuthis dupiniana* d'Orbigny, pp. 377, 378, pl. 12, figs. 1-5.

1966 *Conoteuthis dupiniana* Jeletzky, p. 151, pl. 18, fig. 2A-H; Pl. 24, fig. 1A-G.

*Type specimen.* The writer was unable to find the two cotypes of *Conoteuthis dupiniana* mentioned by d'Orbigny (1842, p. 377) in d'Orbigny's collections at the Muséum National d'Histoire Naturelle, Paris. The whereabouts of these cotypes are unknown according to Dr. J. Sornay of that museum (pers. comm. 1964) and they are presumed lost. A neotype cannot be selected at present as all French specimens studied by the writer are not from the type locality mentioned by d'Orbigny (1842, p. 377) but from Aptian beds of Gurgy near Auxerre (Yonne).

*Material.* Five unnumbered specimens from Collection Pictet in palaeontological collections of the Muséum de Histoire Naturelle, Geneva, Switzerland. These specimens are from Gurgy (Yonne). Two specimens (nos. 37881 and C46812) from Gurgy, near Auxerre, in palaeontological collections of British Museum (Natural History), London, England. One specimen (C58037) from Lower Greensand, Lower Crackers bed, Atherfield, Isle of Wight, in the collections of the British Museum (Natural History), which was figured and described by Jeletzky (1966).

*Description.* Shell small, very sturdy and short, broadly conical in the lateral and dorso-ventral aspects. All specimens studied are fragmentary and unsuitable for measurement. The largest specimen available (Pl. 25, fig. 4A-I; Jeletzky, 1966, pl. 18, fig. 2) is estimated to be about 40 mm long with an adoral dorso-ventral diameter of about 19 mm. This results in an estimated coefficient of elongation of 2.0 to 2.5. The rate of adapical tapering in the ventral and lateral aspects remain approximately the same throughout the known length of the shell



TEXT-FIG. 3. Camera-lucida drawing of the apical part of the specimen C.46812 of *Conoteuthis dupiniana* d'Orbigny 1842 reproduced in Pl. 21, fig. 2A-H. The most apical part of this adapically almost complete shell was restored using the apical angle and the height of the most adapical preserved camerae as a guide. A somewhat oblique dorsal view,  $\times 25$  (approx.). Note the *Diplobelus*-like appearance of all mid-dorsal saddles of the suture lines.

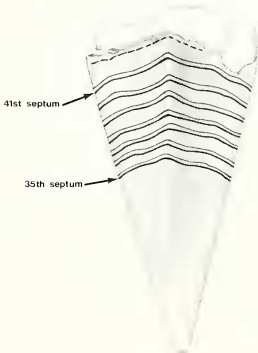


(phragmocone and paper-thin guard), except for the irregularities of outline described below. The conical lateral outline of the shell is distinctly asymmetrical because of a feeble to marked adventral (endogastric) curvature of its posterior part. This curvature results in a feebly to markedly concave ventral outline and a convex dorsal outline of the corresponding parts of the shell (Pl. 25, figs. 1C, D, H, I, 2B, G, 3B, C, H, 4C). No additional endo- or exogastric bends, such as occur in *Vectibelus vectensis* (see there), are superposed on this endogastric curvature in any of the specimens studied. The strength of the endogastric curvature varies from slight in the more slender specimens (e.g. C46812 and the unnumbered Geneva specimens; Pl. 25, fig. 2B, G) to marked in the most sturdy and short specimens (e.g. C58037; Pl. 25, 4B, G, H, or no. 37881; Pl. 25, fig. 3B, C, H). The dorso-ventral apical angle ranges from possibly 25 degrees (probably too low as measured) in the somewhat deformed specimen C46812 (Pl. 21, fig. 2) and definitely 33 degrees (in specimen no. 37881; Pl. 21, fig. 3H) to about 38 degrees (reliable measurement in undeformed specimen C58037; Pl. 25, fig. 4B, G, H). This increase of the apical angle appears to be correlative with the increase in size of the specimens and is assumed to reflect ontogenetic changes of *C. dupiniana* shell.

The ventral and dorsal outlines of the shell are symmetrically conical (e.g. Pl. 21, figs. 1A, G, 2A, F, 3A, G; Pl. 25, fig. 4A, C, I), except when posthumously deformed (e.g. Pl. 21, fig. 4A, B). Cross-section varies from a moderately compressed oval, as in the missing original of d'Orbigny (1842, pl. 12, fig. 5) or the British specimen C58037 (Pl. 25, fig. 4D, E), to an almost perfectly rounded circle (e.g. Pl. 21, fig. 3E). The observed depressed (Pl. 21, fig. 2D) to egg-shaped cross-sections of some Swiss specimens appear to be attributable to their post-mortem deformation. All specimens studied are completely septate phragmocones lacking the earliest camerae and the protoconch.

**Suture line.** As indicated by C46812 (Pl. 21, fig. 2H and text-figs. 3, 4) and an unfigured Swiss specimen, which is almost complete adapically, the earliest observed dorsal saddle of *C. dupiniana* is not yet distinctly angular. This only slightly arched saddle (estimated to be the twentieth from the protoconch; see text-fig. 3) has adorally convex flanks and only differs from the early *Diplobelus* saddles (Pl. 25, figs. 2, 3) in its distinctly lesser height. This *Diplobelus*-like dorsal saddle persists to the estimated thirtieth camera (text-fig. 3) and then changes gradually into a sharp-topped, relatively narrower saddle with distinctly adapically convex flanks in the next ten to fifteen sutures (text-figs. 4, 5). The resulting chevron-like dorsal saddle persists to the latest growth stages available (e.g. to the estimated sixtieth to seventieth camerae; Pl. 21, figs. 1J, K, 3I; Pl. 25, fig. 4C, I; text-figs. 4, 5), just as it does in *V. vectensis* (Pl. 24, fig. 1L).

The dorsal saddle merges imperceptibly into a broad, slightly depressed dorso-lateral lobe, which occupies most of the dorso-lateral segment of the phragmocone (text-fig. 5). This lobe is approximately symmetrical in the early growth stages (text-fig. 3) but becomes distinctly asymmetrical later (text-fig. 5) because of a strongly elevated chevron-like appearance of the advanced dorsal saddle. It merges, in turn, into a similarly broad, slightly but regularly arched dorso-lateral saddle which occupies the remnant of the dorso-lateral segment and



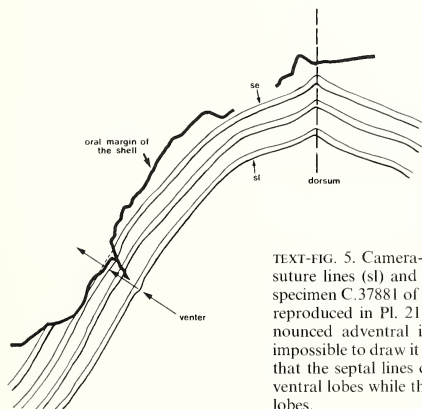
TEXT-FIG. 4. Camera-lucida drawing of the oral part of C.46812, *Conoteuthis dupiniana* d'Orbigny, 1842 reproduced in Pl. 21, fig. 2A-H. Dorsal view,  $\times 12$ . This drawing supplements that of text-fig. 3 and illustrates the rapid transformation of *Diplobelus*-like mid-dorsal saddles of the suture line into typical *Conoteuthis*-like saddles in the interval between 35th and 41st camerae.



the adjacent part of the lateral segment. This symmetrical saddle grades imperceptibly into the lateral lobe, which is similar to the dorso-lateral lobe in its width, shape, and proportions. The lateral lobe occupies the bulk of the lateral segment and grades into the ventro-lateral saddle. The latter occupies most of the adventral segment and is similar to the dorso-lateral saddle, except in the relatively shortened and steepened appearance of its adventral flank (text-fig. 5). This flank merges into a shallow but well-expressed, round-bottomed ventral lobe, the width of which does not exceed one-fifth of that of the lateral lobe. The relatively small width of the ventral lobe accounts for its prominence (text-fig. 5), although it is not much more depressed than the lateral or dorso-lateral lobes. The suture lines of *C. dupiniana* slope adventrally at angles from 15 to 20 degrees (Pl. 21, figs. 1H, I, 2G, 3H, Pl. 25, fig. 4G, H) at all investigated growth stages. No ontogenetic changes in the shape and prominence of any sutural elements were noted, except for the changes in the shape of the dorsal saddle. The septal lines of *C. dupiniana* closely parallel the adjacent suture lines, except on the venter where they either do not form any ventral lobes or form barely perceptible adapical bends (text-fig. 5). The distance between the suture lines and the septal lines comprises about one-sixth of the height of corresponding camerae in all specimens studied. This distance does not seem to change in the course of ontogeny.

**Internal structure.** The oval, dorso-ventrally elongate siphuncle of *C. dupiniana* is rather small in relation to the dorso-ventral diameter of the phragmocone. In specimen C58037 (Pl. 25, fig. 4D) where the siphuncle is best displayed, it comprises about one-ninth of that diameter at the apical end. However, the ratio decreases to about one-tenth of the dorso-ventral diameter at the oral end of that specimen (Pl. 25, fig. 4E). The siphuncle does not touch the inner surface of the phragmocone in undeformed specimens so that no siphonal lobe develops there. However, this phenomenon was observed in some deformed specimens. The internal structure of the phragmocone of *C. dupiniana* was described and illustrated by Jeletzky (1966, p. 151, Pl. 24, fig. 1A-G) on the basis of a thin section of the four most adapical camerae of specimen C58037. No additional information has become available since then. The height of camerae fluctuates between one-twelfth and one-fourteenth of their dorso-ventral diameters in the material studied (Jeletzky, 1966, p. 151, pl. 24, fig. 1A).

Most examples of *C. dupiniana* are either isolated phragmocones (e.g. the originals of d'Orbigny, 1842, pl. 12, figs. 1-5 or C37881, Pl. 21, fig. 3G-I) or phragmocones covered by the conotheca only (Pl. 25, fig. 4G, H, I). The conotheca is a layer 0.2- to 0.5-mm-thick porcellaneous-like and transparent to semitransparent. The suture lines and septal lines are mostly clearly visible through it (Pl. 25, fig. 4G-I). Faint to well-defined, thin conothecal growth lines cover the surface of the conotheca in the best-preserved examples (Pl. 25, fig. 4G-I). The pattern of conothecal striae shown in d'Orbigny's drawings (1842, pl. 12, figs. 3, 4) agrees closely with that observed in all the best specimens studied (e.g. Pl. 25, fig. 4G-I). These striae are subhorizontal on the ventral and ventro-lateral parts of the phragmocone. Then they turn gradually adorally on its midflanks, forming angles of 40 to 50 degrees with the axis. Still closer to the mediodorsal keel these lines gradually steepen until they become sublongitudinal



TEXT-FIG. 5. Camera-lucida drawing of the three most oral suture lines (sl) and the associated septal lines (se) of the specimen C.37881 of *Conoteuthis dupiniana* d'Orbigny, 1842 reproduced in Pl. 21, fig. 1A-K,  $\times 24$ . Because of the pronounced adventral inclination of this suture line it was impossible to draw it approximately on the same level. Note that the septal lines cross the venter without forming mid-ventral lobes while the associated suture lines do form such lobes.

in its proximity. This results in adapically convex, hyperbolar, conothecal striae. The striae do not appear to become exactly longitudinal even on the crest of the keel where they form angles of less than 5 degrees with the axis of the shell. Furthermore, unlike the conothecal striae of *Pavlovitueuthis cantiana* and *V. vectensis*, those of *C. dupiniana* do not turn around rapidly, but gradually within the keel. This indicates that the rhachis-like median field of *C. dupiniana*'s proostracum was very narrow, possessed slightly adorally convergent flanks, and ended in a long sharp tip. This median field may have been longer than the median fields of the proostraca of *Pavlovitueuthis* and *Vectibulus*, which have narrowly rounded oral ends.

The surface of the conotheca and that of the external cast of the phragmocone are transversally corrugated. Like the phragmocone of *Groenlandibulus rosenkrantzi* (Jeletzky, 1966, p. 98), that of the *C. dupiniana* contracts over the septa and expands between them. The resulting round-bottomed troughs and ridges are best visible in Pl. 21, fig. 1k. They are also clearly visible in the less satisfactorily preserved specimens 37881 (Pl. 21, fig. 3G-I) and C46812 (Pl. 21, fig. 2f-h).

The mediodorsal longitudinal keel occurs in all representatives of *C. dupiniana* studied. When the guard is absent, this keel is a simple, slightly to moderately elevated (up to about 1 mm high, see Pl. 25, fig. 4d) gable-like structure. The keel's flanks form angles of 25 to 30 degrees with adjacent, regularly rounded surface of the shell (Pl. 21, figs. 1k, 2i, 3t; Pl. 25, fig. 4d). The keel of the best-preserved moulds of phragmocones (Pl. 21, fig. 1k, 3t) is flanked by a slightly impressed, ill-defined longitudinal furrow on each side. These fine, round-bottomed furrows delimit the keel from the regularly rounded shell surface throughout its length. Such moulds of the keel are topped by a narrow flat zone extending over its whole length. The mediodorsal keel of those specimens where the phragmocone is covered by a well-preserved conotheca differs in its sharp-topped appearance and increased height (Pl. 25, figs. 4c, i). This indicates that the keel proper consists of distinctly thickened, sharp-topped conotheca.

*Guard.* The surface of well-preserved conotheca is overlain locally by a thin but morphologically distinctive shell layer in one undeformed (Pl. 21, fig. 1k) and another strongly deformed (Pl. 21, fig. 4a-d) Swiss specimen. This layer, which is sharply delimited from the underlying conotheca, is interpreted herein as a strongly attenuated guard because of its superposition on the conotheca and structural features described below. Scattered patches of the guard preserved on oral parts of these two shells (Pl. 21, fig. 1k) are always paper-thin (about 0.2 mm). However, the guard gradually thickens apicalward until it becomes at least 0.5 mm thick on their most apical preserved parts (Pl. 21, figs. 1k, 4c). These thickened adapical parts of the guard (altered to a dark-brown, ferruginous or phosphatic compound in Pl. 21, fig. 4) exhibit a distinct radial striation suggestive of its primary radially prismatic structure. Small patches of the guard preserved on the anterior part of the shell may exhibit faint replicas of the septa, including the septal lines. However, neither the septal nor the conothecal pattern reappears on the smooth surface of the thickened guard covering the apical part of the shells concerned.

The guard covers the mediodorsal keel of the phragmocone and conotheca, reproducing its shape approximately. However, the surface of the resulting mediodorsal keel of the guard is sculptured (Pl. 21, figs. 1k, 4d). This sculpture, which appears to be totally absent on the underlying keels, is centred in a median longitudinal furrow, which is 0.2 to 0.25 mm wide, similarly deep and round-bottomed. This furrow is flanked by about equally wide, round-topped longitudinal ridges, which are about 0.2 mm high. These ridges are flanked, in turn, by feebly outwardly sloping outer longitudinal zones of the keel's 'roof'. These outer zones are three to four times wider than either the adjacent ridges or the median furrow. They are indistinctly limited from the narrower, more steeply inclined slopes of the keel (Pl. 21, fig. 1k). These slopes appear to merge imperceptibly into the regularly rounded surface of the shell.

The mediodorsal keel of the guard has exactly the same appearance in both specimens of *C. dupiniana* where its fragments are preserved. This indicates that its sculptural details are constant morphological features of a suprageneric rank. In the almost completely preserved specimen C46812 (text-fig. 3) the mediodorsal keel appears at the level of the estimated twenty-second septum. It may have been present even further adapically in this specimen (Pl. 21, fig. 2i), the most apical part of which is unfortunately deeply eroded. The drawings of d'Orbigny (1842, pl. 12, figs. 2, 4) suggest the extension of the mediodorsal keel to the very apex of the shell. Taken in themselves, these drawings are unreliable. D'Orbigny's drawings are commonly idealized and/or strongly reconstructed. In this instance, however, the essential correctness of his drawings is confirmed by the almost completely adapically preserved, and mostly guard-covered specimen reproduced in Pl. 21, fig. 4a, b. In this specimen the mediodorsal keel of the guard is clearly discernible at the level about 1 mm adorally of its incomplete, guard-covered apex which appears to correspond to the fourth or fifth camera of the complete shell. The keel could have extended right to the apex also in this specimen. The evidence available suggests, therefore, that the mediodorsal keel of *C. dupiniana* extended on to the most apical part of the shell and reached to its apical

tip as indicated in d'Orbigny's drawings. His drawings also suggest that the keel ornamenting the surface of the conotheca and that ornamenting the external cast of the phragmocone extended to the apex of the shell. Except for the mediodorsal keel and the faint replica of septa locally visible on the anterior two-thirds to three-quarters of the shell, the surface of the guard of *C. dupiniana* appears to be completely smooth.

*Discussion.* *C. dupiniana* differs from the only other *Conoteuthis* species known, *C. woodwardi* Spath (1939, p. 3, fig. 2*d, e*), in its more slender shape, less prominent mediodorsal ridge, and a considerably less marked adventral curvature of the posterior part of the shell. Since *C. woodwardi* is also considerably younger, these morphological distinctions appear to be sufficient for its specific differentiation from *C. dupiniana*. *C.? syriaca* (Roger, 1944) (Jeletzky, 1966, pp. 151, 152) cannot be compared with either *C. dupiniana* or *C. woodwardi* at present as the morphology of its shell is unknown and the validity of its reconstruction attempted by Roger (1944, fig. 3) is highly suspect. *C.? syriaca* is therefore only questionably assigned to *Conoteuthis* by the writer. '*C.? rennieri*' Spath, 1939 is excluded from the genus *Conoteuthis* for reasons presented below.

*Stratigraphical and geographical range.* In the present, extremely meagre, state of our knowledge *C. dupiniana* is restricted to the Aptian rocks of Anglo-Paris Basin. The British specimen reproduced in Pl. 25, fig. 4 is derived from the Crackers bed of Forbesi Zone according to Casey (1961, p. 501). The exact levels of the French specimens studied are unknown.

#### *Pavloviteuthis* Shimansky, 1957

*Type species.* *Pavloviteuthis kabanovi* Shimansky, 1957.

*Diagnosis.* Diplobelidae with straight to slightly adventrally incurved, moderately wide, conical phragmocone which may be either laterally compressed and broadly oval or egg-shaped (with the ventral segment being widened and more obtuse) in cross-section; the height of camerae comprise one-sixth to one-seventh of their dorso-ventral diameter; subtransversal to slightly adventrally sloping suture lines consist of two saddles and two lobes only and have a broad, gently arched, and flat-topped mediodorsal saddle; the sheath-like guard with few layers paralleling the surface of the phragmocone, lacking any appreciable bulges or depressions, and exhibiting a belemnite-like radially prismatic structure; the guard's surface is finely ribbed or very finely striated; poorly understood proostracum appears to have a rhachis-like median field which is relatively wider than that of *Conoteuthis* and *Vectibelus* but has a *Vectibelus*-like, narrowly rounded oral end; phragmocone's structure is unknown. Mid- to late Early Cretaceous.

*Geographic range.* Central part of European Russia (Volga area) and eastern England (Folkestone).

*Discussion.* The British representative of *Pavloviteuthis* described below is important in elucidating a number of critical morphological features of this rare and poorly known diplobeline genus. As pointed out by Jeletzky (1966, p. 152), the original description of the genus and its monotypic type species *P. kabanovi* provided a bare minimum of information needed to establish the validity of the genus and left its taxonomic position in considerable doubt. The subtransversal orientation of the suture line and the broadly rounded shape of the dorsal saddle indicate the reference of '*Conoteuthis cantiana*' Spath, 1939 to *Pavloviteuthis* Shimansky in spite of its considerably younger age. The absence of a chevron-like or narrowly rounded, high dorsal saddle in the suture line of '*C. cantiana*' in combination with a much greater height of its camerae suffices to exclude it from the genera *Diplobelus*, *Conoteuthis*, *Vectibelus*, and *Chalalabelus*. The diplobeline affinities of *Pavloviteuthis* are now confirmed by the discovery of a diagnostic, rapidly adorally tapering proostracum ending in a very narrow, subparallel-sided, rhachis-like median field in *P. cantiana* (text-figs. 7, 8; Pl. 23, fig. 3*A, B*). This proostracum is similar to that of *Vectibelus vectensis* in the shape of its oral end. This morphological feature differentiates *Pavloviteuthis* from otherwise similar Belemnoteuthididae and Chondroteuthididae and excludes it from the Belemnitina.

The very low, exceedingly broad and flat-topped dorsal saddle of *Pavloviteuthis* (text-figs. 7, 8) is unlike the relatively much higher, regularly but narrowly rounded dorsal saddle of *Diplobelus* (Pl. 25,

figs. 2, 3). This saddle is even more unlike the narrow and chevron-like advanced dorsal saddles of *Conoteuthis* and *Chalalabelus* (text-figs. 4, 5, 12f). It differs from the earliest known juvenile dorsal saddles of *Conoteuthis* (text-fig. 3) in a greater width and flat-topped appearance. The ventral lobe of *Pavloviteuthis* is closely similar to that of *Conoteuthis* and *Vectibelus* (Pl. 21, fig. 1G; text-fig. 5; and Pl. 24, fig. 1J; text-fig. 10). The slightly adventrally sloping sutures and septal lines of both known *Pavloviteuthis* species (Pl. 22, fig. 1C, D; Shimansky, 1954, Pl. 12, figs. 4, 5a, and 1957, p. 44) differ markedly from much stronger sloping sutures and septal lines of *Conoteuthis*, *Vectibelus*, and *Chalalabelus*. However, they resemble closely the suture lines and, apparently, the septal lines of *Diplobelus* in this respect (Pl. 25, fig. 1B).

*Pavloviteuthis cantiana* (Spath, 1939)

Plate 22, fig. 1A-K; Plate 23, fig. 1A-F; Plate 25, fig. 5

1939 *Conoteuthis cantiana* Spath, pp. 3, 4 (explanation of text-fig. 2), fig. 2f, g.

**Diagnosis.** *Pavloviteuthis* species characterized by the absence of fine ribbing on the surface of the guard and its replacement by an extremely fine, closely spaced, sublongitudinal or adapically obliquely converging striation forming a herring-bone pattern visible at magnification of only six to ten times.

**Type specimen.** The unique specimen no. 37844 preserved in the palaeontological collections of British Museum (Natural History), is the holotype of *Pavloviteuthis cantiana* (Spath 1939) by monotypy.

**Description.** The deformed and cracked surface of the guard appears to be completely smooth to the naked eye, except for a few irregularly shaped, sublongitudinal furrows. The largest of these furrows extends longitudinally across the posterior half of the right flank (Pl. 22, fig. 1C). This almost straight furrow is situated somewhat dorsally and consists of two relatively widened and deepened sections separated by a shallower section 5 to 6 mm long. The furrow rapidly shallows and then disappears on the most apical part of the flank and ends abruptly in its middle just below a deep, post-mortem depression where the guard is stripped off (Pl. 22, fig. 1C). This furrow is evidently a real feature, and not the result of some injury suffered by the animal, because there is another similar on the left flank. The well-preserved and guard-covered posterior part of that flank bears a

EXPLANATION OF PLATE 22

Fig. 1A-K. *Pavloviteuthis cantiana* (Spath, 1939). Holotype, B.M. (N.H.) 37844. Gault Fm. (Albian), Folkestone, England; referred to by S. P. Woodward (1896). A, a somewhat oblique ventral view,  $\times 1$ ; s—position of the siphuncle at the oral end. B, dorsal view,  $\times 1$ . Note the asymmetrically located, possibly pathological, longitudinal furrows on the dorsum and the visible part of the left flank. C, left lateral view,  $\times 1$ ; v—venter; d—dorsum. D, right lateral view (in relation to venter),  $\times 1$ . Note the irregularly shaped dorso-lateral furrow which is also visible on the left side of fig. 1B. E, cross-section of the fragmentary oral end,  $\times 1$ ; v—venter. Dorso-ventrally elongated, elliptical, hard marginal siphuncle (s) is visible in the mid-ventral position. F, apical view of the apical end,  $\times 1$ ; v—venter. G, ventral view as in fig. 1A but  $\times 6$  to illustrate fine longitudinal striation of the surface of the guard. Oral half of specimen is partly devoid of the guard (g) and conotheca (c) and exposes the phragmocone (ph) while the apical half is completely covered by well-preserved, thin guard (g). H, lateral view of the completely guard-covered posterior half of the right flank shown in fig. 1D,  $\times 6$ , showing fine striation of surface, and dorso-lateral furrow (f). Specimen further prepared to show suture lines, hyperbolic zones, and conothecal lines on Pl. 23, fig. 3A, B, and fig. 1K. I, oblique dorsal view as in fig. 1B,  $\times 6$  to illustrate the oblique, fine striation of surface and absence of mediodorsal keel. The striae of the flanks are inclined toward the mid-dorsal plane where they meet forming a 'herring-bone' pattern. J, apical view as in fig. 1F but  $\times 6$  to illustrate the thickness of the guard (g) in the apical break; s—siphuncle; v—venter. K, same view as in fig. 1J but approx.  $\times 25$  and with the most adapical few millimetres of the guard stripped off on the left flank and dorsum. Thin guard remnants (g) show belemnite-like structure of radial calcitic prisms crossing ill-developed, concentric growth lines. The dorso-ventrally elongated, oval, hard marginal siphuncle(s) is clearly visible at the bottom of the photograph.

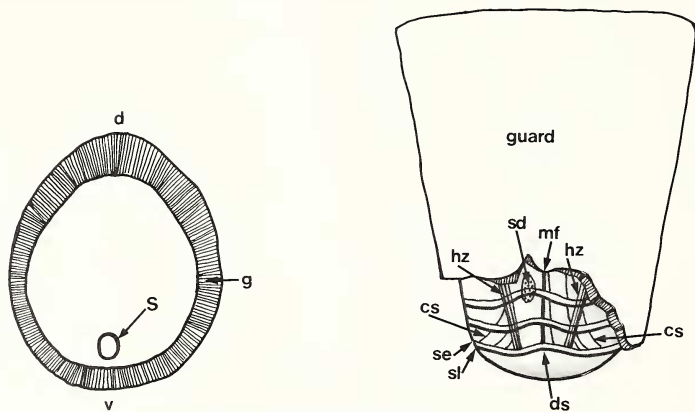


JELETSKY, Cretaceous belemnites



longitudinal furrow about 5 mm long, which is considerably finer and more shallow than its counterpart and is situated more adorsally than the latter (Pl. 22, fig. 1D, H). The furrow of the left flank is superimposed almost exactly on the left hyperbolar zone of the phragmocone. Adventurally of it is a depression of irregular shape, poorly impressed, 0.5 to 1.0 mm wide, which extends right through the undeformed posterior half of the shell (Pl. 22, fig. 1D, H). The very fine, somewhat oblique striae covering the flank are more strongly expressed on the bottom of this depression than around it. A third irregular, wavering, sublongitudinal furrow occurs in the middle of the dorsum (Pl. 22, fig. 1B, I). This furrow consists also of two relatively deepened sections separated by a slightly impressed intermediate section. The adapical deepened section is situated approximately in the middle of the dorsum and above the mediadorsal furrow of the phragmocone. This mediadorsal furrow of the guard peters out about 5 mm from the apical end of the shell. Like the lateral furrows, this furrow is a real feature unrelated to the surrounding, obviously post-mortem cracks and deformations of the guard. Because of their subsymmetrical arrangement, the three furrows on the specimen are interpreted tentatively as somewhat irregularly expressed anatomical features of its guard. A pathological origin cannot be ruled out at present. Pending the discovery of additional specimens of *P. cantiana*, these furrows were excluded from its diagnosis.

Most of the better-preserved areas of the guard's surface show a characteristic pattern of very fine, even and closely spaced, sublongitudinal to feebly oblique striae at a magnification of  $\times 6$  to  $\times 10$  (Pl. 22, fig. 1G, I; Pl. 23, fig. 1A, C). These striae, which are quite invisible to the naked eye, are longitudinally oriented and so fine on the venter that they are barely visible  $\times 25$ . The striae are strongly expressed on the flanks and dorsum. On the flanks they are feebly inclined adorsally forming angles of 5 to 10 degrees with the longitudinal axis of the shell. The striae of the flanks finally converge in the middle of the dorsum where they meet on the sides of the above-described mediadorsal, longitudinal furrow (Pl. 22, fig. 1I). On the apical third of the dorsum, where the furrow is absent, the converging striae either intertwine irregularly or become deflected adapically and acquire a subparallel orientation in a narrow mediadorsal zone. The sheath-like guard permits an imperfect view of the closely spaced, underlying septa on the anterior part of the shell where it is paper-thin. The surface of the guard is feebly transversely corrugated on that part of the shell reflecting the transverse corrugation of the underlying



Camera-lucida drawings of the holotype of *Pavloviteuthis cantiana* (Spath, 1939). C.37844 reproduced in Pl. 22, fig. 1K and Pl. 23, fig. 1A-D.

TEXT-FIG. 6 (left). Cross-section of the apical end reproduced in Pl. 22, fig. 1K,  $\times 10$ , showing true shape and proportions of the cross-section. The photograph is less egg-shaped as it was somewhat tilted in relation to the camera.

TEXT-FIG. 7 (right). Dorsal surface of the phragmocone exposed at the apical end of the specimen reproduced in Pl. 23, fig. 1A-D,  $\times 25$ . Abbreviations: s—siphuncle; g—guard; mf—mediadorsal furrow; ds—dorsal saddle; hz—hyperbolar zones of the proostracum; cs—conothecal striae; sd—secondary pyrite.



phragmocone. This corrugation disappears entirely on the posterior two-thirds of the shell where the guard thickens appreciably.

The surface of the guard does not exhibit any traces of the pattern of the underlying conothecal striae, in spite of its thinness. This probably reflects an extremely faint nature of the latter. The long, conical shell appears to be perfectly symmetrical in dorso-ventral aspect, except for post-mortem deformations (Pl. 22, fig. 1G, I). The lateral aspect is distinctly asymmetrical because of a feeble adventral curvature of the posterior half (Pl. 22, fig. 1C, D, H). Because of this curvature, the ventral side of the shell is feebly concave while its dorsal side is feebly convex. The preserved, entirely septate part of the shell is about 25.7 mm long; it is estimated to lack 6 to 8 mm at the apical end. The lateral apical angle of the posterior part of the shell is 25 or 26 degrees (Pl. 22, fig. 1C, D, H). The apical cross-section is only feebly compressed (coefficient of compression about 0.9), egg-shaped. Its dorsal segment is narrower than the almost perfectly rounded ventral segment and its middle part protrudes appreciably between almost straight-flanked dorso-lateral quadrants (Pl. 22, fig. 1K). However, the protruding mid-dorsal segment remains regularly rounded throughout and there is no trace of a *Conoteuthis*-like keel either on the surface of the phragmocone or on that of the overlying thin guard (Pl. 22, fig. 1J, K; text-fig. 6).

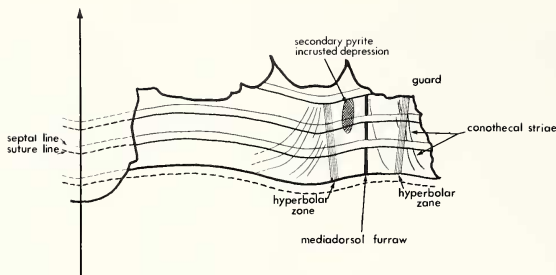
The oral part of the shell is too incomplete and too strongly deformed for its shape and cross-section to be confidently restored. However, the shape and proportions of its partly preserved oral cross-section (Pl. 22, fig. 1E) probably were similar to those of the completely preserved and undeformed apical cross-section. The apical angle apparently remained the same throughout the shell's length and there is no reason to infer the presence of a *Conoteuthis*-like mediodorsal keel anywhere on the anterior part of the shell.

*Internal structure.* The guard is only 0.6 mm thick in the broken apical cross-section, except in the mediodorsal zone where it is 0.8 to 0.9 mm thick (Pl. 22, fig. 1K; text-fig. 6). The guard thins out gradually oralward until its fragments preserved on the oral quarter of the shell become 0.1 mm thick or less (Pl. 22, fig. 1G). The addorsally contracted cross-section of the shell is more strongly expressed on the surface of the guard than on the underlying phragmocone because of a considerable thickening of the guard in the mid-dorsal zone as compared with the flanks. The apical cross-section of the guard, which was photographed before and after the removal of the strongly pyritized most apical 3 to 4 mm of the guard (Pl. 22, fig. 1J, K), exhibits a characteristically belemnite-like texture consisting of dense, radially prismatically arranged calcitic crystals intersecting several very thin, alternately darker and lighter-coloured concentric growth layers. This radial texture is locally discernible in the cross-sections of attenuated guard on the oral quarter of the shell. The colour of the guard varies from completely clouded and white to semitransparent and either honey-coloured or dull brown. These modifications apparently reflect its lesser or stronger weathering. The guard is invariably very sharply delimited from the underlying conotheca. The paper-thin (0.2 to 0.25 mm thick) conotheca covering the apical end of the specimen (Pl. 23, fig. 1A-F) has a massive, brownish-grey to dull brown-coloured and semitransparent appearance. Its surface has a nacreous lustre. Fragments of paper-thin conotheca occur on the oral half of the specimen, where the equally thin guard is mostly stripped (Pl. 22, fig. 1G), and are dull-white and clouded to semitransparent.

The siphuncle is markedly oval and compressed. Its dorso-ventral diameter at the broken-off apical end of the shell is 0.7 mm while the corresponding lateral diameter is 0.4 mm (Pl. 22, fig. 1K), and the flanks are almost flat in contrast with the almost regularly rounded dorsum and venter. The siphuncle almost touches the ventral wall of the phragmocone. The shape of the siphuncle at the fragmentary oral end of the shell is similar to that exposed at the apical end. At the oral end the siphuncle has a dorso-ventral diameter of 1.3 mm and a lateral diameter of 0.7 mm (Pl. 22, fig. 1E).

The undeformed camera at the apical end is 0.9 mm high and is 5.5 mm long at the base in a dorso-ventral direction. Therefore, its height comprises about one-sixth of its length. The next adoral camera is about 1.0 mm high and about 6.0 mm long and so has about the same ratio of height to length. This ratio is considerably greater than the ratios characteristic of *Conoteuthis* (one-twelfth to one-fourteenth) and *Vectibelus* (about one-eighth).

The earliest preserved suture lines show a dorsal saddle which is very broad, feebly arched, broadly rounded on the flanks and flat-topped. This saddle occupies most of the dorsal quadrant of the phragmocone (Pl. 23, fig. 1A, B; text-figs. 7, 8). This early dorsal saddle is flanked by a fairly markedly depressed but wide and flat-bottomed dorso-lateral lobe, which is only slightly narrower than the dorsal saddle and occupies most of the dorso-lateral segment of the phragmocone. This lobe is followed, in turn, by a much broader and only slightly arched lateral saddle which occupies most of the remaining two-thirds of the phragmocone's flank and about one-third of its ventro-lateral segment (Pl. 23, fig. 1C, F; text-fig. 8). The lateral saddle is somewhat asymmetrical, its addorsal flank being more oblique and shorter than the barely perceptible adventral flank. The latter merges imperceptibly into only slightly depressed but relatively narrow and regularly rounded rather than

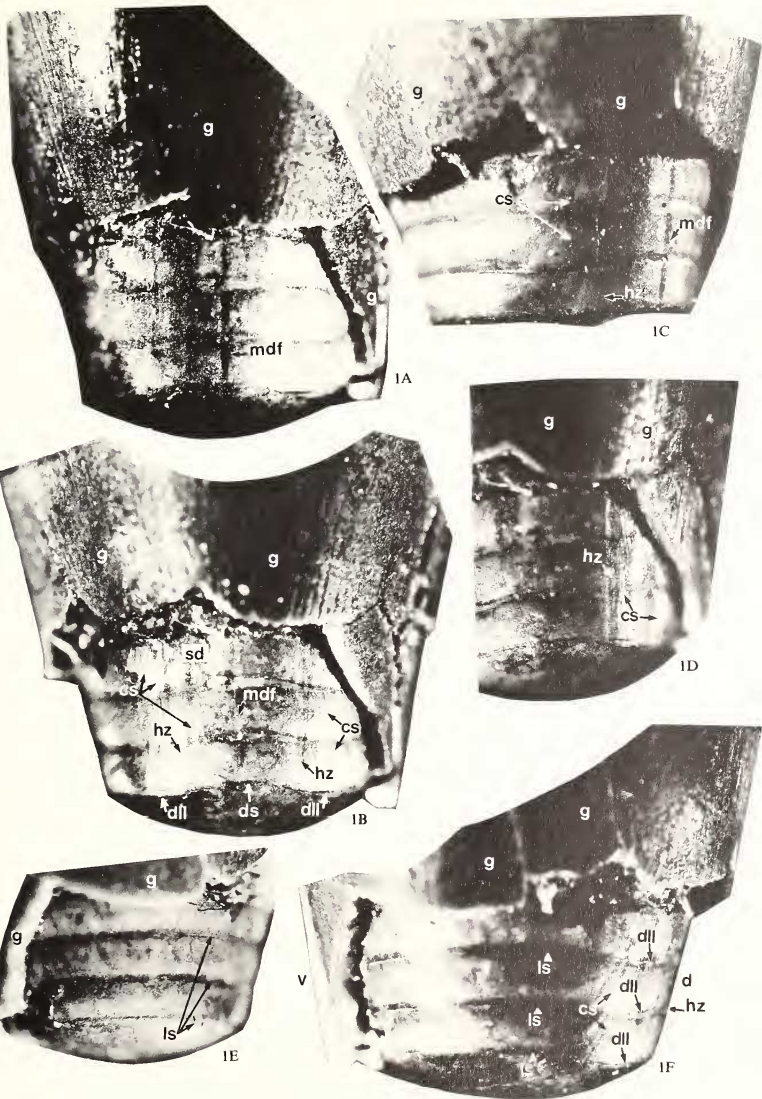


TEXT-FIG. 8. Camera-lucida drawing of three most apical sutures and septal lines of the holotype of *Pavloviteuthis cantiana* (Spath, 1939). B.M. (N.M.) 37844,  $\times 50$ . Overlapping segments of these sutures and septal lines are reproduced photographically in Pl. 23, fig. 1A-F and their dorsal parts are reproduced on a smaller scale in text-fig. 7. The guard-covered ventral segments of suture lines are shown in dotted lines using the corresponding segments exposed in text-fig. 9 as a guide. The mediadorsal furrow subdivides the dorsal saddle in two. An arrow marks the position of the mid-venter.

flat-bottomed ventral lobe, which occupies the middle part of the ventral segment (Pl. 22, fig. 1G; text-fig. 8). The septal lines, which did not reproduce clearly in most of the large-scale photographs taken of the earliest preserved camerae of the holotype (e.g. Pl. 23, fig. 1A, C, D, F), are reproduced graphically in text-figs. 7 and 8. These early septal lines parallel the adjacent suture lines throughout their extent and form ventral lobes which duplicate those of the suture lines. The distance between the adjacent sutures and septal lines comprises 20 to 25% of the height of exposed early camerae. The space confined between the adjacent suture and septal line in each camera was presumably occupied by a relatively narrow mural part of the corresponding septa. The early sutures and septal lines slope feebly adventrally forming angles of 80 to 85 degrees with the long axis of the shell. On the middle and oral parts the sutures are incomplete but they appear unchanged to the oral rim. This is best illustrated by the sutures and septal lines which are clearly visible through the semitransparent conotheca on the flanks and venter of the oral third of the shell (Pl. 22, fig. 1C, G, I; text-fig. 9). The distances between the adjacent sutures and septal lines comprise again 20 to 25% of the heights of the corresponding camerae (e.g. 2 mm out of 9 mm in the eighth camera from the oral end; text-fig. 9) and their pattern is the same. Dorsal parts of these advanced sutures and septal lines are invariably poorly preserved and more or less deformed. However, their

#### EXPLANATION OF PLATE 23

Fig. 1A-F. *Pavloviteuthis cantiana* (Spath, 1939). Holotype, B.M. (N.H.) C.37844. Gault Formation (Albian). Folkestone, England. Strongly magnified photographs of the apical end of the specimen which exhibits the surface of phragmocone overlain by a thin, semitransparent inner layer of the conotheca. A, dorsal view,  $\times 20$ . Focused on the mediadorsal furrow (mdf). The surface of the guard (g) is covered by oblique fine striae which form a herringbone pattern. B, as in fig. 1A, but coated with ammonium chloride to show hyperbolar zones (hz) and conothecal striae (cs). Secondary pyrite-incrustated depression (sd) of the phragmocone is visible between the indistinctly reproduced mediadorsal furrow (mdf) and the left hyperbolar zone. Note dorso-lateral lobes (dll) and the dorsal saddle (ds). C, left dorso-lateral view,  $\times 20$ , with the left hyperbolar zone (hz) and adjacent conothecal striae (cs) in the centre. Medio-dorsal furrow (mdf) on right. D, right dorso-lateral view,  $\times 20$ , showing right hyperbolar zone (hz) and adjacent conothecal striae (cs). E, ventro-lateral view,  $\times 20$ , with the crest of the lateral saddle (ls) on the right. F, lateral view,  $\times 20$ . Ventral side (v) on the left. Crest of lateral saddle (ls) in centre, trough of dorso-lateral lobe (dll) and conothecal striae (cs) on right. Left hyperbolar zone (hz) is at right margin.



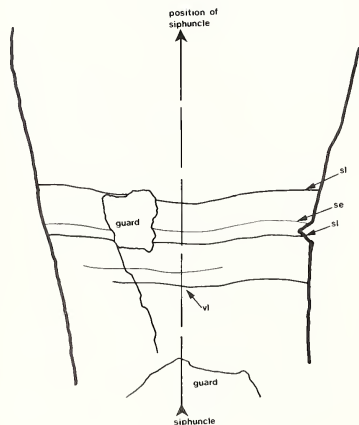
JELETSKY, Cretaceous belemnites

dorsal saddles appear to be just as low and broadly rounded as those of the earliest preserved sutures and septal lines (Pl. 22, fig. 1f; Pl. 25, fig. 5).

The surface of the conotheca exposed on the most apical part of the shell (Pl. 23, fig. 1A-F; text-figs. 7, 8) exhibits a somewhat peculiar, though generally diplobeline, conothecal pattern. The ventralmost visible parts of these conothecal striae (Pl. 23, fig. 1E; text-fig. 8) are oriented almost transversely. The striae then turn adorally in the middle of each axis of the shell. Then the striae gradually turn adorally on the middle and addorsal parts of each flank until they become steeply addorsally inclined (forming angles of 15 to 20 degrees with the long axis of the shell; Pl. 23, fig. 1C, D, F; text-fig. 8) in dorso-lateral positions. The resulting bends are regularly hyperbolic in shape. When the striae become steeply addorsally inclined they cross single symmetrically situated, sublongitudinal furrows, which converge apicalward forming 5 to 10 degrees angles with the shell's axis. These paired dorso-lateral furrows of the conotheca are 0.12 to 0.2 mm wide; they are shallow, flat-bottomed, and steep-sided (Pl. 23, fig. 1C, D, F; text-figs. 7, 8). Because of their position and relationship with the conothecal striae, these furrows are hyperbolic zones of a belemnite type. The conothecal striae cross these hyperbolic zones on the previous, steeply addorsally inclined course. Then they continue to steepen gradually until their angles with the longitudinal axis of the shell decrease to 5-10 degrees in the close proximity of the mid-dorsal plane which is marked by the mediadorsal furrow described below (text-figs. 7, 8). This is indicated by the orientation of a considerable number of partially preserved conothecal striae observed within the slightly elevated, 1.2- to 1.25-mm-wide mid-dorsal zone confined by the hyperbolic zones. These striae, none of which is clearly discernible in the large-scale photographs of Plate 23, are very faint and visible only in a strong lateral light at magnifications of 25 to 50 times. Some of them were drawn using camera lucida and are indicated in text-figs. 7 and 8. It is notable that after forming 5- to 10-degree angles with the shell's axis near the mid-dorsal plane the striae turn around and become less steep yet closer to this plane. This suggests that the tip of the rapidly adorally narrowing and generally speaking rhachis-like median field outlined by these striae was narrowly rounded like that of the *Vectibelus* (compare text-fig. 11) rather than sharpened like that of the *Conoteuthis* (Pl. 25, fig. 4f).

A fine (0.05 to 0.075 mm wide) but deeply depressed, distinctly segmented, longitudinal furrow occurs in the mid-dorsum of the conotheca (Pl. 23, fig. 1A-C; text-figs. 7, 8). This furrow, which appears to be narrowly U-like in cross-section, resembles closely the so-called normal line (also known as septal furrow or dorsal furrow; see Teichert in Teichert *et al.*, 1964, p. K.30) of fossil nautiloids and aulacocerids and is interpreted as its homologue. It occurs in the middle of the slightly elevated mid-dorsal zone confined between the hyperbolic zones.

A depression 0.05 to 0.07 mm wide and about 2 mm long, oval and pyrite-incrustated, occurs between the mediadorsal furrow and the left hyperbolic zone (Pl. 23, fig. 1B; text-fig. 7), and appears to be either a pathological feature or a post-mortem deformation of the conotheca and phragmocoene.



TEXT-FIG. 9. Camera-lucida drawing of the suture lines and septal lines exposed on the ventral side of the oral third of the holotype of *Payloviteuthis cantiana* (Spath, 1939), C.37844,  $\times 25$ . The reproduced lines are those visible in the seventh and eighth camerae from the oral end of the specimen in Pl. 22, fig. 1G. vl—ventral lobe. Other abbreviations as in text-fig. 7.

*Discussion.* Except for the three possibly pathological furrows, the guard surface of *P. cantiana* (Spath, 1939) is smooth to the naked eye. Magnifications at  $\times 6$  or greater show the characteristic striations. The surface of an appreciably thicker guard of *P. kabanovi* is ornamented by fine, irregularly wavy riblets, which are clearly visible to the naked eye (Shimansky, 1954, Pl. XII, fig. 5a; 1957, p. 44). Considering the difference in age of *P. kabanovi* and *P. cantiana*, this distinction is judged to be ample for their specific differentiation. The somewhat lesser apical angle of *P. kabanovi*, which measures 21 degrees as against 25–26 degrees in *P. cantiana*, may not be significant on the specific level.

*Stratigraphic and geographic range.* The only known representative of *P. cantiana* (Spath, 1939) was found in the Albian part of the Gault Formation at Folkestone, England (Spath, 1939, p. 3). No data about the more exact horizon and age of this specimen are available to the writer.

### *Vectibelus* gen. nov.

*Derivation of name.* From *Vectis Insula*, a Roman name for the Isle of Wight.

*Type species.* *Conoteuthis vectensis* Spath 1939. Designated herein.

*Diagnosis.* Diplobelidae in which the posterior part of the shell, including the guard, is S-like incurved when viewed laterally; the guard is paper-thin except around protoconch where it is appreciably thickened and forms an addorsally oblique, small postalveolar spine; the *Conoteuthis*-like ornamented mediodorsal, longitudinal keel is restricted to the anterior part of the guard; it peters out in its middle part leaving the posterior part of the dorsum keelless and regularly rounded; the generally *Conoteuthis*-like median field of the proostracum has a narrowly rounded, instead of sharpened, oral end.

*Stratigraphical range.* Spath (1939, p. 3), states that the only known representative of *Vectibelus* (i.e. of '*C.*' *vectensis* Spath 1939) was found either in the Lower Lobster Bed or in the Crackers Bed of the Atherfield Clay, Lower Greensand (see Casey, 1961, table 1). These beds are almost the only units exposed at Atherfield Point, Isle of Wight, where the holotype was found. If so, this specimen is from the *Deshayesites callidiscus* Subzone of *D. forbesi* Zone of Casey (1961, table 1).

*Discussion.* The unique specimen on which *Vectibelus* gen. nov. is based is well preserved, and non-pathological; its morphological peculiarity justifies the erection of the new taxon on a single specimen in this case. It would be unsafe to base the new genus *Vectibelus* on the S-like recurved appearance of its shell alone, in spite of a perfect symmetry of the phragmocone and the guard of the specimen, including its superficially sepiid-like apical spine. Other peculiar morphological features are not pathological in nature because of their ontogenetically restricted character and an obvious correlation with one another. The most important of these features is the restriction of the mediodorsal keel of the guard to the anterior part of the shell and its rapid disappearance on the posterior part of the dorsum. These ontogenetic changes are accompanied by marked changes in the appearance of the underlying dorsal saddle of the suture line, which is clearly visible through the thin, semi-transparent guard, except in the most apical 3 to 4 mm of the phragmocone. The dorsal saddle remains generally round-topped, broad, and entirely *Diplobelus*-like (compare Pl. 24, fig. 1L with Pl. 25, figs. 2, 3 and Zittel, 1968, pl. I, fig. 14a) all over the regularly rounded, non-keeled adapical part of the dorsum while becoming progressively higher and narrower. Further adorally on the keeled part of the dorsum the dorsal saddle rapidly becomes more and more adorally sharpened and chevron-like. These ontogenetic changes of the mediodorsal zone of the guard and the underlying dorsal saddle of the suture line can hardly be assumed to be pathological features because of their obvious regularity and coupling. This ontogenetic development contrasts strongly with that of *Conoteuthis* as restricted herein, where the sharp-topped mediodorsal keel of the phragmocone (but not the anteriorly sharpened, chevron-like dorsal saddle of the suture line) appears at the earliest growth stages known, which are inferred to be situated only a few camerae adorally of the protoconch (Pl. 21, fig. 2H; text-fig. 3).



Other distinctive and taxonomically high-ranking (Jeletzky, 1966, p. 8; Pl. 24, fig. 11; text-fig. 11) morphological features of *Vectibelus* gen. nov. include:

1. The adorally tapering but narrowly rounded appearance of the oral end of the median field of the proostracum, which contrasts with the sharpened oral end of that field in *Conoteuthis* s. restr. and, apparently, of the *Diplobelus* and *Chalalabelus* gen. nov. as well. Only *Pavloviteuthis* possesses a similarly rounded oral end of the median field. However, it differs from *Vectibelus* fundamentally in the absence of a mediodorsal keel, and a chevron-like dorsal saddle.
2. The presence of a unique sculpture on the mediodorsal keel of the guard (Pl. 24, fig. 1G, i; text-fig. 11), differing from that of the *Conoteuthis* keel (Pl. 21, fig. 1K; text-figs. 3, 4) in a relatively greater width and an almost flat-bottomed (feebly concave) appearance of the median furrow. Furthermore, the flanking, longitudinal ridges of the *Vectibelus* keel are relatively more narrow than the furrow, sharply delimited from its feebly concave bottom part, and sharp-topped. The outer longitudinal zones of these two keels are similar, except that the adjoining slopes of the keel are considerably wider in *Vectibelus* in comparison with the keel slopes of the corresponding growth stages of *Conoteuthis*. Consequently, the keel of *Vectibelus* is a much more prominent structure than that of the *Conoteuthis*, in spite of its relatively lesser length. The genera *Diplobelus* and *Chalalabelus* gen. nov. differ from *Vectibelus* gen. nov. in a complete absence of mediodorsal keels on the surface of their guards. The genus *Pavloviteuthis* differs in lacking such keels not only on the surface of the guard but on the surface of the phragmocone as well.
3. The rapid thickening of the most apical part of the otherwise skin-like guard ending in an obliquely adorsally directed, small postalveolar spine. This guard differs radically from stout, apically rounded guards of *Diplobelus* and *Chalalabelus* gen. nov. However, we do not know apical parts of the guards of *Conoteuthis* s. restr. and *Pavloviteuthis*. Hence it is difficult to apprise the taxonomic significance of this feature.
4. The uniquely large apical angle of the phragmocone. Though difficult to measure because of a recurved and bulging lateral profile of the *Vectibelus* phragmocone, this angle, when measured in the lateral aspect, is estimated to be 40 to 45 degrees. This value is considerably greater than that characteristic of the genera *Conoteuthis* s. restr., *Diplobelus*, and *Pavloviteuthis*. Only *Chalalabelus* possesses a comparably large apical angle of the phragmocone.

Most of these peculiar morphological features of *Vectibelus vectensis* appear to be of supra-specific rank. Taken together, they are enough to rule out the assignment of the holotype to any other known Diplobelina genus.

### *Vectibelus vectensis* (Spath, 1939)

Plate 24, fig. 1A-K; text-figs. 10, 11

1939 *Conoteuthis vectensis* Spath, pp. 3, 4 (explanation of fig. 2), fig. 2*h*, *i*.

*Type specimen.* British Museum (Natural History), London, 48619, holotype of *Vectibelus vectensis* (Spath 1939) by monotypy. Locality and age as above. I have recently been informed that this specimen is lost.

*Description.* The guard is about 19.5 mm long when measured from the tip of the spine to the alveolar rim of the dorsum. Its maximum measurable dorso-ventral diameter situated at the alveolar rim about 9 mm adapically of the oral end of the specimen is 10.5 mm. The maximum measurable lateral diameter at about the same level is 9.0 mm. Both diameters were measured perpendicular to the axis of the shell. Only dorso-lateral and dorsal segments of the shell are preserved above this level. The compressed (coefficient of compression is about 0.86) most adoral preserved cross-section of the shell gradually becomes about equidimensional closer to the apex (Pl. 4, fig. 1E, H). This cross-section remains regularly rounded throughout. Adapically of the level of maximum measurable diameters the shell contracts rapidly and increasingly fast in dorso-lateral aspect to a level about 3.5 mm above apex. This results in a symmetrical, slightly convex outline throughout this interval (Pl. 24, fig. 1A, D, G). Further towards the apex the rate of contraction decreases noticeably and progressively to the tip of the apical spine. This results in a symmetrical but slightly concave outline of the adapical region of the shell (Pl. 24, fig. 1A, D, G). The change from a convex to a concave outline distorts the generally broadly conical dorso-ventral outline of the shell which has an average apical angle of 45 to 50 degrees. The slightly convex dorso-lateral outline of the shell is maintained to the fragmentary oral rim above the level of maximum measurable diameters. The broadly conical shape of the shell in lateral aspect is complicated by curving first markedly exogastrally in the anterior two-thirds, and then markedly endogastrally in the posterior third. Finally, the short apical spine



curves markedly exogastrically once more (Pl. 24, fig. 1b, c, f). This S-like, lateral outline is more noticeable on the ventral than on the dorsal side. The latter shows the endogastric curve and the second exogastric curve while being moderately and regularly convex throughout the anterior three-quarters of its preserved length (Pl. 24, fig. 1f). The dorso-ventral apical angle, which is difficult to measure because of the outline of the shell, is about 40 to 45 degrees. The well-defined apical spine, which begins just below the protoconch, is rounded in cross-section, about 2.5 mm long and tapers regularly adapically all the way to its rounded tip. This spine is directed obliquely addorsally forming an angle of 20 to 25 degrees with the longitudinal axis of the shell (Pl. 24, fig. 1b, c, f).

The dorsal side of the completely guard-covered shell has a median longitudinal keel which begins at the oral rim and extends, gradually diminishing in height, adapically over its anterior part (Pl. 24, fig. 1g, i; text-fig. 11). The keel ends at a level about 11.5 mm below the oral rim leaving the remaining part of the mediadorsal zone more or less regularly rounded, except for a faint suggestion of a longitudinal ridge near the keel's end. This rounded mediadorsal zone merges imperceptibly into the regularly rounded posterior parts of the flanks. The generally roof-like mediadorsal keel is about 2 mm wide and 1 mm high at the oral rim of the shell where its somewhat concave sides converge at equal, moderate angles toward the flattened top. The top is about 1 mm wide at the oral rim of the shell but narrows gradually apicalward and then disappears just before the keel's apical end (Pl. 24, fig. 1i; text-fig. 11). The middle zone of this essentially flat top is occupied by a shallow median furrow with a gently concave bottom, which comprises somewhat less than one-half of its width. This longitudinal furrow extends to about 3 mm before the apical end of the keel, gradually narrowing and shallowing apicalward. Single, very fine, sharp-topped longitudinal ridges flank the furrow on each side. These ridges are flanked, in turn, by slightly outwardly slanted, round-edged outer zones of the flat top, which grade imperceptibly into the sloping flanks of the keel (Pl. 24, fig. 1i; text-fig. 11).

The mediadorsal keel of *V. vectensis* is only comparable to the fragments of the mediadorsal keel of *Conoteuthis dupiniana* preserved on the guard-covered parts of its phragmocone (Pl. 21, figs. 1k, 4d). The morphology of these keels was compared in the discussion of *Vectibehus* gen. nov. The shape and ornamentation of the mediadorsal keel of the phragmocone of *V. vectensis* remains unknown.

The guard's surface on both sides of the keel is ornamented by a series of closely spaced, distinct but fine, round-bottomed and round-topped furrows and ridges, which appear to reproduce the pattern of the conothecal growth lines occurring on the underlying surface of the phragmocone (Pl. 24, fig. 1g, i; text-fig. 11). This furrow-and-ridge pattern is exactly symmetrical on both sides of the keel. The most adlateral parts of all furrows and ridges are horizontally to subhorizontally oriented. Closer to the keel they gradually acquire a more and more adventrally inclined direction until they become sublongitudinal in its close proximity. This results in furrows and ridges forming regular obliquely addorsally convex hyperbolic curves (Pl. 24, fig. 1i; text-fig. 11). Still closer to the keel most of the furrows and ridges disappear while others weaken markedly. Those few of them that remain visible recurve addorsally on the keel's slopes and then appear to cross the keel forming narrow, parabolic loops, which are only observable at high magnification and are mostly too faint to be photographed (compare Pl. 24, fig. 1i with text-fig. 11). These furrows and ridges are restricted to the anterior half of the guard's dorsum where its thickness ranges from paper-thin to less than 1 mm. The recurrence of conothecal striae on the surface of this part of the guard of *V. vectensis* appears to be the first such record in the order Belemnitida. As such, it is of an unusual interest. This phenomenon is, however, not uncommon in the order Aulacocerida. Jeletzky (1966, pp. 17, 18) has recorded the most important instances of the recurrence of conothecal growth lines in Aulacocerida and offered an explanation of this phenomenon, which appears to be equally applicable to *V. vectensis*. Except for the mediadorsal keel and the recurrent conothecal striae, the surface of the guard appears to be completely smooth to the naked eye; minute corrugations and pitting seen at  $\times 10$  magnification may be because of weathering (Pl. 24, fig. 1i).

*Internal morphology.* The buff- to honey-coloured matter of the guard is dense and normally calcified throughout. In the cross-section at the oral rim of the shell the guard exhibits a typical belemnitid structure consisting of fine, radially prismatic crystals of calcite which pierce less distinctly defined, thin, alternately darker and lighter coloured concentric growth lines. The guard is 0.1 mm or less thick on the most oral preserved, dorsal part of the alveolar rim, which attests to an almost complete preservation of this part of the shell. The guard thickens gradually and very slowly on the more adapically situated lateral parts of the alveolar rim until it becomes 0.5 to 0.7 mm thick on its ventral part which is situated slightly above the shell's middle. Then the guard continues to thicken very slowly to the level 2-3 mm above the base of the apical spine. Its thickness probably does not exceed 0.8 mm at the latter level. Because of the thinness of the guard it is semitransparent all the way from the oral rim to the level 2-3 mm above the base of the spine and so affords a fair view of the underlying camerae and suture lines (Pl. 24, fig. 1l-k). Further apicalward the guard becomes non-transparent because of an appreciable thickening; it is assumed to be about 1.0 mm thick just before the base of the spine. The earliest

few suture lines and the protoconch are invisible because of this thickening of the guard. However, it is possible to see the outline of the protoconch using a strong spotlight (text-fig. 10). The apical spine of *V. vectensis* apparently possesses a well-developed apical line as the cross-section of its broken-off tip exhibits a tiny, centrally situated, pit-like hollow (Pl. 24, fig. 11). Such hollows commonly occur in normal belemnitids because of a more intensive weathering of the guard's matter along their apical line.

The conotheca of *V. vectensis* was only seen exposed in cross-section at its oral rim and marginally in tiny (up to 5–6 mm long and 1–2 mm wide) fragments protruding at the alveolar rim from underneath the paper-thin to 0·7-mm-thick guard. This dense and apparently structureless conotheca is approximately 0·05 to 0·075 mm thick, dull-white coloured, and semitransparent; it has a porcellaneous shine and is sharply delimited from the overlying guard. The specimen is septate throughout, the septa extending right to the oral rim of its dorsal side where the guard is paper-thin (Pl. 24, fig. 11). The camerae of the phragmocone and the suture lines are clearly visible through the semitransparent guard, except on the most apical 2 to 3 mm of the chambered shell. The three most oral preserved camerae are only 0·5 to 0·6 mm high (on the ventral side) and about 10·5 mm long in dorso-ventral direction. The resulting height/width ratio of one-eighteenth to one-twentieth is the smallest known in the suborder. The earliest few suture lines and the protoconch are hidden from view because of an appreciable thickening of the most apical part of the guard. However, the use of a strong spotlight reveals that the regularly rounded ventral part of the guard situated just adorally of the apical spine reproduces closely the shape of the corresponding part of the underlying protoconch. This spherical protoconch is unusually large for the Belemnitida and, like the apical part of the phragmocone, adventrally inclined. This inclination is in opposition to the addorsal inclination of the apical spine, which is superposed on the protoconch in a somewhat sepiid-like

## EXPLANATION OF PLATE 24

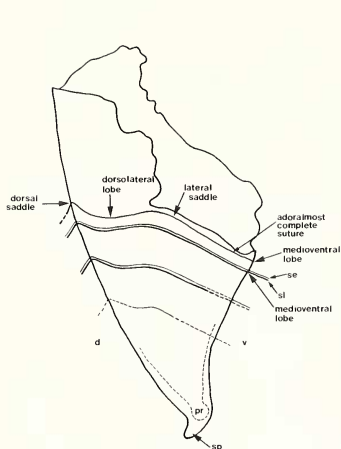
Figs. 1A–L. *Vectibelus vectensis* (Spath, 1939). Holotype, B.M. (N.H.) C.48619. Aptian, Isle of Wight, Atherfield Point. A, ventral view,  $\times 1$ . B, left lateral (in relation to the venter) view; v—venter; d—dorsum,  $\times 1$ . C, right lateral view (in relation to the venter); same symbols as in fig. 1B. D, dorsal view,  $\times 1$ . Mediodorsal keel (mdk) restricted to oral half of specimen. E, apical view of apical end,  $\times 1$ ; v—venter; d—dorsum. F, left lateral view,  $\times 4$  to show fine structure. G, dorsal view,  $\times 3$  to show fine structure. H, view as fig. 1E,  $\times 3$  to show small, rounded depression marking the position of the apical line (al). I, dorsal view of the guard,  $\times 6$ , showing finely corrugated (c) and commonly pitted (?weathered) appearance of the guard's surface; fmk—central furrow of mediodorsal keel; rmk—flanking ridges of mediodorsal keel; cs—impressions of conothecal striae on the surface of the thin guard covering the anterior part of the phragmocone; smk—lateral slope of mediodorsal keel; mf—marginal furrows of mediodorsal keel; tcs—top part of conothecal striae. Narrow tops of conothecal striae (tcs) locally visible on surface of mediodorsal keel near oral margin. Other symbols as in fig. 1G and text-fig. 11. J–K, the same views as in fig. 1A, C, and D respectively,  $\times 3$  to show suture lines. See text-fig. 10 for interpretation of structural details.

Figs. 2A–H. *Belemnoteuthis antiqua* Pearce, 1947. B.M. (N.H.) C.37440. Lower Callovian, Kellaways Rock, Wiltshire. A, ventral view,  $\times 1$ . B, left lateral view (in relation to the venter),  $\times 1$ ; v—venter; d—dorsum. C, right lateral view (in relation to the venter),  $\times 1$ , same symbols as in fig. 1B. D, dorsal view,  $\times 1$ . E, same view as in fig. 2A but  $\times 3$  to elucidate fine structural details. F, same view as in fig. 2B,  $\times 3$ ; ph—exposed surface of phragmocone with suture lines and septal lines; c—patches of conotheca covering the surface of phragmocone; g—thin sheath-like guard covering both the conotheca and the phragmocone; dk—lateral surface of right dorsal keel. Other symbols as in fig. 1B and 1C. G, dorsal view  $\times 3$ ; mdf—mediodorsal furrow; ldk—left dorsal keel; rdk—right dorsal keel; other symbols as in fig. 2F. H, cross-section of the oral end,  $\times 1$ , part of the ventral rim including the siphuncle broken off.

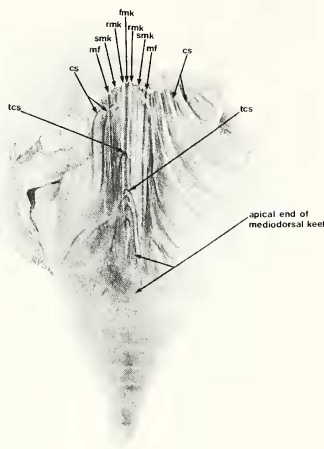
Figs. 3A–J. *Chalalabelus* aff. *C. remiei* (Spath, 1939). B.M. (N.H.) C. 58036, coll. C. W. Wright, ?Mid-Barremian, ?Cement Beds B, Speeton, Yorkshire. A, ventral view,  $\times 1$ . B, left lateral view (in relation to the venter),  $\times 1$ ; v—venter; d—dorsum; irregular welts suggest lifetime injury. C, right lateral view (in relation to the venter),  $\times 1$ . D, dorsal view,  $\times 1$ . E, cross-section of alveolar end,  $\times 1$ , same symbols as in fig. 3B. F, same view as in fig. 3E, but  $\times 3$  to show belemnitid structure of guard. G, cross-section of apical end,  $\times 3$  to show irregular shape of guard and its growth layers, indicating that apical part of guard was damaged and then healed. H, ventral view of rubber mould of the alveolar cavity,  $\times 1$ . I, dorsal view of the same mould,  $\times 1$ . J, lateral view of the same mould,  $\times 1$ ; v—venter; d—dorsum. Note the exceptionally large apical angle combined with the pronounced adventral curvature of the alveolus.



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TEXT-FIG. 10. Camera-lucida drawing of the suture lines, septal lines, and protoconch of the holotype of *Vectibelus vectensis* (Spath, 1939) reproduced in Pl. 24, fig. 1A-K,  $\times 12$ . Lateral view with the addition of the parts of dorsal saddle and ventral lobe not visible in this aspect. All suture and septal lines and protoconch somewhat schematic as they were obscured by the thin guard. The protoconch was drawn using very strong spot light. Abbreviations: sl—suture line; se—septal line; pr—protoconch; sp—apical spine of the guard; d—dorsum; v—venter.



TEXT-FIG. 11. Diagrammatic drawing of medio-dorsal sculptural elements visible on the surface of the guard of the holotype of *Vectibelus vectensis* (Spath, 1939) reproduced in Pl. 24, fig. 1G, I. Dorsal view,  $\times 6$ . cs—impressions of conothecal striae on the surface of paper-thin guard; tcs—top parts of the conothecal striae outlining the oral end of the proostracum; fmk—central furrow of mediodorsal keel; rmk—flanking ridge of mediodorsal keel; smk—lateral slope of mediodorsal keel; mf—marginal furrows of mediodorsal keel.

fashion (Pl. 24, fig. 1F; text-fig. 10). All observable suture lines are strongly oblique, sloping adventrally, and forming angles from 25 to 30 degrees with the longitudinal axis of the shell (Pl. 24, fig. 1K). The highest points of the suture lines are situated mid-dorsally atop of markedly arched to chevron-like dorsal saddles. So far as it is possible to discern through the semitransparent cover of the guard, the dorsal saddle occupies about one-third of the dorsum (text-fig. 10). It exhibits strong and regular ontogenetic changes. Like the mediodorsal keel, the adorsally sharpened, chevron-like dorsal saddle resembling that of *Conoteuthis* is restricted to the anterior part of the shell presumably representing the adult growth stage of the animal. This saddle gradually develops out of a broadly rounded, *Diplobelus*-like, dorsal saddle which characterizes the earlier keelless growth stages of the shell. The dorsal saddle merges into a considerably broader dorso-lateral lobe which occupies the remaining two-thirds of the dorsal segment of the phragmocone. This lobe is markedly depressed, broadly round-bottomed, and all but symmetrical. It merges imperceptibly into an extremely wide and pronouncedly asymmetrical lateral saddle which occupies all of the dorso-lateral and lateral segments of the phragmocone and most of its ventral segment (text-fig. 10). The regularly arched and broadly round-topped adorsal flank and crest of this saddle are approximately restricted to the dorso-lateral segment of the phragmocone. They are stronger but shorter than the adventral flank of the saddle, which slopes evenly and gently across the flank and most of the venter. In most of the suture lines the lateral saddle can only be differentiated from the ventral lobe because of their complete flattening in the mid-venter. One could say that these suture lines lack a discernible ventral lobe. Only two or

three most oral suture lines begin to exhibit slightly depressed, but narrow and shallow U-like ventral lobes in the mid-venter, which resemble the more strongly expressed ventral lobe of *Conoteuthis* (text-fig. 5).

The septal lines follow exactly the courses of the adjacent suture lines, except that no discernible ventral lobes appear in the two or three oralmost septal lines (text-fig. 10). The distance between the adjacent suture and septal line comprises about one-sixth of the height of the corresponding camera. The siphuncle was not observed. Nor was it possible to see any details of the internal septal structure.

*Chalalabelus* gen. nov.

*Type species.* *Conoteuthis renniei* Spath, 1939.

*Diagnosis.* Diplobelidae which are *Vectibelus*-like in the shape and proportions of phragmocone, *Conoteuthis*-like in characters of suture line and presence of mediiodorsal keel on the phragmocone, and *Diplobelus*-like in shape and proportions of guard.

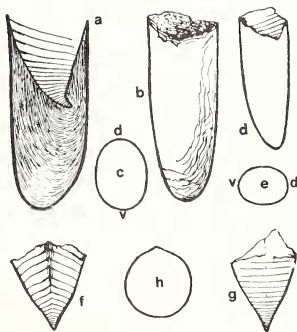
*Derivation of name.* The genus is named after the fossil locality Chalala, near Delagoa Bay, Mozambique, where the type material of the type species was found (Spath, 1939, p. 2).

*Discussion.* Spath (1939, p. 2) placed *Chalalabelus renniei* into *Conoteuthis* as he assumed the isolated phragmocones of type specimens of *C. dupiniana* to be enclosed by similarly thick and stout guards. However, Spath (1939, p. 3) noted a thickening of the test towards the apex of the phragmocone in his *Conoteuthis cantiana* from the English Albian and concluded that 'the presence of such a test in the English form (not preserved in *C. dupiniana*) might suggest that there was some reason after all for the original restoration of *Conoteuthis*, and that *Chalalabelus renniei* may belong to a different genus, closer to *Diploconus*.' My studies indicate that *Chalalabelus* gen. nov. based on *C. renniei* (Spath 1939) is the most peculiar representative of the Cretaceous Diplobelina, which differs from all other Cretaceous representatives of the suborder in the presence of a stout and thick walled, adapically rounded guard, which lacks any kind of ornament.

The breviconic, strongly adventrally incurved, obtuse phragmocone of *Chalalabelus* contrasts with the much more longiconic, slender to moderately obtuse, slightly to moderately adventrally incurved phragmocones of *Pavloviteuthis* and *Conoteuthis*. Finally, *Chalalabelus* differs from *Conoteuthis* and *Vectibelus* in a complete absence of a longitudinal keel on the surface of the guard, in spite of the presence of a *Conoteuthis*-like keel on the surface of the phragmocone and conotheca. These morphological distinctions, which are illustrated by text-figs. 12a-12g, are judged to be enough for a generic separation of *Chalalabelus* from *Conoteuthis*, *Pavloviteuthis* and *Vectibelus*.

The guard of *Chalalabelus* resembles closely that of the Late Jurassic *Diplobelus* Naef, 1926 (= *Diploconus* Zittel, 1868). However, it has a relatively much longer postalveolar region because of

TEXT-FIG. 12. *Chalalabelus renniei* (Spath, 1939). Aptian, Chalala, Delagoa Bay, Mozambique. a, Idealized cross-section of the holotype (no. 215) showing the phragmocone and the lamellar structure of the guard; b, c, complete paratype I (no. 217); b, ventral view; c, sectional outline; d, e, paratype II (no. 205) with phragmocone partly exposed; d, lateral view; e, sectional outline. f-h, idealized dorsal (f) and ventral (g) views of an isolated alveolar cast (no. 140) with sectional outline (h). All figures are photographs of *Conoteuthis renniei* Spath (1939, text-figs. 1a-e, 2a-c). v—venter; d—dorsum.





the relatively much shallower alveolus (compare Zittel, 1868, pl. 1, figs. 14d, e, f and this paper Pl. 25, fig. 1A, B with Spath, 1939, fig. 1a and this paper text-fig. 12a). *Chalalabelus* also differs from *Diplobelus* in a strong adventral curvature of the apical part of its phragmocone (the phragmocone of *Diplobelus* is almost straight; Pl. 25, fig. 1A, B), a much greater apical angle of the alveolus (45 to 50 degrees against 24 to 26 degrees in *Diplobelus*) and a regularly oval, compressed cross-section of the guard. These distinctions are enough for a generic separation of *Chalalabelus* from *Diplobelus* in spite of their sharing the complete absence of a longitudinal, mediodorsal keel on the surface of the guard.

*Stratigraphic range.* According to Spath (1939, p. 2) *C. renniei* was found in Aptian rocks. The English *Chalalabelus* aff. *C. renniei* described below was found on the surface of mid-Barremian Cement Beds of the Speeton section and is assumed to be of that age. These skimpy data suggest that *Chalalabelus* ranged at least from mid-Barremian to Aptian time.

Its geographic range is thus from south-western Africa to eastern England.

*Chalalabelus* aff. *C. renniei* (Spath, 1939)

Plate 24, figs. 3A–J, text-fig. 12

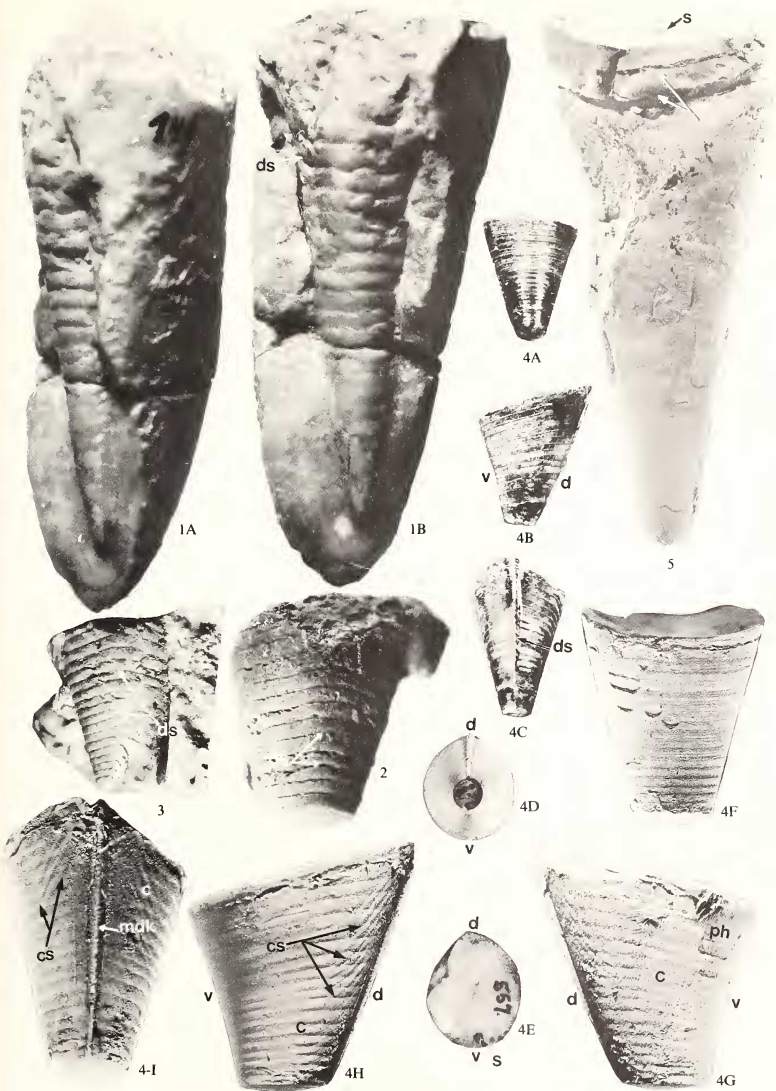
*Material.* One fragmentary, presumably pathological guard B.M. (N.H.) C.58036, coll. Mr. C. W. Wright.

*Description.* The only known representative of *C.* aff. *C. renniei* resembles closely *C. renniei* (Spath, 1939) in most discernible features of its phragmocone and guard. These include such taxonomically important features as the presence of the short, rather stout (coefficient of elongation is about 2) guard with bluntly rounded apex in combination with short, dorsally carinated phragmocone. The surface of the guard appears to be smooth except for the irregular welts and depressions described below. The phragmocone (Pl. 24, fig. 3j) is similar to that of *C. renniei* (text-fig. 12a, f–h) in being sharply incurved adventrally in the apical quarter and in having an apical angle (in lateral aspect) of about 45 degrees. These features indicate that the English guard is congeneric with Mozambican type material of *Chalalabelus* gen. nov.

EXPLANATION OF PLATE 25

- Fig. 1A–B. *Diplobelus belemnitoides* (Zittel, 1868). Paratype. Upper Tithonian, white limestone of Stramberg, Stramberg, Czechoslovakia. Specimen drawn by Zittel (1868, pl. 1, fig. 14f),  $\times 3.3$  (the original is 41 mm long). A, ventral view. B, lateral view.
- Fig. 2. *Diplobelus belemnitoides* (Zittel 1868). Tithonian, Kotzobenz near Teschen, Czechoslovakia. Dorsal view of medium-sized fragmentary phragmocone preserved entirely as an external cast (i.e. devoid of conotheca),  $\times 2.5$  (the original is 17 mm long). Although the fragment represents the anterior part of the phragmocone, all dorsal saddles of suture lines are broadly rounded.
- Fig. 3. *Diplobelus belemnitoides* (Zittel, 1868). Tithonian, Ernstbrünner Limestone, Klafferbrunn near Ernstbrunn, Niederösterreich. Dorsal view of fragmentary early part of phragmocone, external cast,  $\times 1.5$ . Specimens in figs. 1–3, Geologische-Paläontologische Abteilung, Naturhistorisches Museum, Vienna, Austria. Photographs by Dr. Fr. Bachmayer.
- Fig. 4A–I. *Conoteuthis dupiniana* d'Orbigny, 1842. Lower Greensand, Crackers bed, Aptian stage, Atherfield (Isle of Wight), SE England. B.M. (N.H.) C58037. A, ventral view,  $\times 2$ . B, lateral view,  $\times 2$ . C, dorsal view,  $\times 2$ . D, apical view,  $\times 2$ . E, oral cross-section,  $\times 2$ . F, ventral view,  $\times 4$  to show fine sculptural details of the conotheca and phragmocone. G, left lateral view,  $\times 4$  to show fine sculptural details of the conotheca and phragmocone. H, right lateral view (the same as in fig. 4B),  $\times 4$  to show fine structural details of the excellently preserved conotheca. I, dorsal view,  $\times 4$  to show fine details of the conotheca and mediodorsal keel. Steeply inclined conothecal striae become almost parallel with the longitudinal axis of the phragmocone on both sides of the keel and maintain this course to its crest. These parts of the striae outline the rhachis-like, orally sharpened median field of the proostracum. Abbreviations in figs. 1–4: v—venter; d—dorsum; ds—dorsal saddle; c—conotheca; ph—phragmocone exposed where the conotheca is absent; cs—conothecal striae; s—siphuncle; mdk—mediodorsal keel.
- Fig. 5. *Pavloviuteuthis cantiana* (Spath, 1939). Holotype. B.M. (N.H.) C.37844. Gault Formation (Albian), Folkestone, England. Dorsal view,  $\times 4$ . Siphuncle visible at the oral end of the specimen permits its exact orientation.





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On the specific level the discernible morphological distinctions of *C. aff. C. renniei* are: 1. Somewhat sturdier proportions of the guard, the restored length of which (about 20 mm) is only two times greater than the maximum dorso-ventral diameter (about 10 mm). The length of nearly complete guards of *C. renniei* (Spath 1939, fig. 1a, b, d) is 2.5 to 3.0 times greater than their maximum dorso-ventral diameter. 2. The approximately symmetrical profile of the apical region in the lateral aspect (Pl. 24, fig. 3B, C). The apical region of the holotype and the small paratype of *C. renniei* (Spath, 1939, fig. 1a, d) are markedly asymmetrical with the apex displaced adorsally. This eccentric apex is considered to be a diagnostic feature of *C. renniei* by Spath (1939, p. 1).

It is difficult to evaluate the taxonomic value of distinctions between *C. aff. C. renniei* and *C. renniei* as its only known representative may be a pathological form. This is indicated by the fact that the guard C.58036 is distinctly asymmetrically shaped (Pl. 24, fig. 3A, G). Furthermore, most of its surface is covered by irregularly shaped bulges and depressions (Pl. 24, figs. 3B, C, G). These irregularities are most pronounced on the flanks of the guard and on its apical surface where the exfoliated concentric growth layers are irregularly bent throughout (Pl. 24, fig. 3G). The apical part of the animal, including the guard, may have been injured. The animal was evidently able to survive the event (a collision or an attack by a predator) and to heal the wounds. But the use of open nomenclature is advisable for this specimen. The palaeogeographical importance of this solitary representative was noted above.

*Locality and age.* The guard is recorded as being derived from the ?Cement Beds B, Speeton, Yorkshire, from float. Hence the uncertainty concerning the exact age. Accepting the derivation of the specimen concerned from the Cement Beds B, it is of the mid-Barremian age.

*Acknowledgements.* For loan of material I thank Dr. E. Lanterno, Dr. M. K. Howarth, Dr. J. Sornay, Mr. C. W. Wright and Professor F. Bachmayer. I thank Mr. L. Bairstow for useful discussion. I am grateful to Mr. M. F. McLaughlin and Mrs. K. Vincent for help in the preparation of the manuscript, and Miss J. White for photography.

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Typescript received 20 May 1979

Revised typescript received 21 January 1980

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